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Martens and fishers in a changing climate

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Abstract

Average global temperatures are projected to rise between 1.1 and 6.4° C by the end of the century. Coupled with changes in precipitation and increasing atmospheric carbon dioxide concentrations, these increases in temperature will alter species distributions and phenologies with cascading effects on ecological communities and ecosystem functions. In this chapter, we investigate how projected changes in climate are likely to affect 4 *Martes* species: American marten (*M. americana*), fisher (*M. pennanti*), stone marten (*M. foina*), and European pine marten (*M. martes*). We review both recent trends in climate and projected future climate changes throughout the geographic ranges of these 4 species and project shifts in their distributions under multiple climate-change scenarios. To provide insights at a finer spatial scale, we describe analyses that have explored the potential effects of climate-driven changes in fire regimes and

fisher habitat in the southern Sierra Nevada Mountains in California. We projected that both North American species will experience northward range shifts during the coming century. Projected climate-driven shifts in the potential ranges of the 2 European species were more complex and more variable. The finer scale analyses for California fisher populations revealed potential changes in forest composition from conifers to mixed-hardwoods in the north, and to mixed-hardwood forests and grasslands and shrublands in the south. Increases in fire frequency and intensity were also projected for the southern Sierra Nevada population. Finally, more-detailed simulations resulted in projected losses of large conifer and hardwood trees as fire severity increased. For fishers in the southern Sierra Nevada, we recommend protecting old-forest habitats through targeted forest-fuel treatment, and applying more liberal fire-suppression policies to naturally ignited fires during moderate weather conditions. Overall, our results suggest that martens and fishers will be highly sensitive to climate change and, as for many species, will likely experience the largest climate impacts at the southernmost latitudes and lowest elevations within their ranges. Furthermore, several marten populations that are currently considered to be at risk of extirpation will likely experience future climates that are outside the range of current climatic conditions.

INTRODUCTION

During the last 100 years, average annual global temperatures have risen 0.7° C (IPCC 2007b), but temperatures have been increasing more rapidly in the recent past. For example, during the last 50 years, average global temperatures have risen twice as fast as over the previous 50 years. This trend in warming is projected to continue into the future and will likely be accompanied by changes in precipitation patterns. Global average surface temperatures are projected to rise between 1.1 and 6.4° C by 2100 (IPCC 2007b). The largest increases are projected for high-

northern latitudes where average annual temperatures may increase by more than 7.5° C. There is far less agreement among projections of future precipitation patterns. In the winter months, climate models generally agree that there will be an increase in precipitation in the mid- to high-northern latitudes. In the summer months, most land masses are projected to experience less precipitation. However, there is less confidence in these projections than for winter projections. Among summer projections, there is more confidence in drying trends projected for Europe, the Mediterranean region, southern Africa, and the northwestern contiguous United States (U.S.) (IPCC 2007b).

These changes have had, and are projected to continue having, profound effects on many other physical processes. For example, recent increases in the size and frequency of fires in the western U.S. have been linked to changing moisture regimes (Westerling et al. 2006). Portions of that area are projected to experience a 2- to 4-fold increase in the frequency of large fires during the coming century (McKenzie et al. 2004). Changes in temperature and precipitation have already had impacts on hydrology (IPCC 2007a). Future changes will likely have even more profound effects on snowpack, the timing and frequency of stream flows, and water availability for many plant and animal species.

Recent trends in climate have also been linked to numerous ecological changes (Parmesan 2006). The best documented of these changes are shifts in species distributions and changes in phenologies (Parmesan and Yohe 2003, Root et al. 2003). Many species have shifted their ranges in accordance with changing temperatures, often resulting in poleward or upward shifts in species distributions (e.g., Moritz et al. 2008). Similarly, changes in the timing of important annual life-history events have occurred that generally correspond with recent trends in climate

change. Flowering in plants, migratory patterns and egg laying in birds, and mating in amphibians have all experienced documented shifts in their phenologies (Parmesan 2006).

In this chapter, we provide an overview of some of the potential impacts of future climate change on the American marten (*Martes americana*), fisher (*M. pennanti*), stone marten (*M. foina*), and European pine marten (*M. martes*). We chose these 4 species because of the availability of detailed data on their current and historical distributions; due to limited data, it was not possible to model potential climate-change impacts on all 8 *Martes* species. We begin by summarizing recent historical and projected future changes in climate across the ranges of these 4 species. We then use bioclimatic models to project broad-scale shifts in their potential geographic distributions. We conclude by using a set of finer scale forest-growth and fire models to examine potential changes in habitat for the fisher in California.

RECENT CHANGES IN CLIMATE

We assessed trends in mean annual temperatures and total annual precipitation from 1950 to 2002 across the current ranges of these 4 species using the Climatic Research Unit (CRU) TS 2.1 monthly climate dataset (Mitchell and Jones 2005). This dataset has a 0.5-degree spatial resolution (grid cells approximately 50 km per side, depending on latitude).

We calculated linear trends in both temperature and precipitation with the Climate Wizard climate-analysis tool using a restricted maximum-likelihood linear-regression analysis method (Girvetz et al. 2009).

American Marten and Fisher

For the American marten and fisher, the largest changes in temperature have occurred in Alaska (marten) and northern Canada (both species). In parts of these regions, mean annual temperatures have increased at a rate of 0.4° C per decade. Changes have been less dramatic in

the eastern and the southernmost portions of the species' ranges where temperatures have generally increased by less than 0.2° C per decade. California, northeastern Quebec, and Newfoundland did not show significant changes in temperature over this 52-year period.

Patterns of recent trends in total annual precipitation within the ranges of the 2 North American species are far less consistent than those of temperature trends. For the American marten, the largest significant increases in precipitation were in the northeastern and north-central parts of its range. Only a few areas in the range (e.g., eastern Alaska and south of James Bay at the southern tip of Hudson Bay) showed significant decreases in precipitation. Decreasing trends in precipitation in other parts of its range were not significant. For the fisher, precipitation has decreased in the extreme northwestern part of its range, and in portions of the north-central part of the range. As with temperature, only a few isolated locations experienced significant decreases in precipitation during this time period.

Stone Marten and European Pine Marten

From 1950 to 2002, temperatures also increased over most of the ranges of stone and pine martens. The strongest trends were in southern France and Spain for the stone marten and in northern Spain, France, Estonia, and Latvia for the pine marten where, in some places, temperatures increased at rates exceeding 0.4° C per decade. Conversely, there were very few places within the ranges of either species that experienced significant trends in precipitation. Both species experienced increases in precipitation in central France and decreases in Slovenia. The pine marten experienced increases in precipitation in Scotland, northern Scandinavia, Estonia, Latvia, Lithuania, and southern Sweden.

PROJECTED CHANGES IN CLIMATE

We assessed projected changes in mean annual temperature and total annual precipitation for all 4 species at the end of the 21st century. We calculated differences between climate averaged over a recent 30-year period (1970-1999) and projected climate averaged over a future 30-year period (2070-2099) using the Climate Wizard climate-analysis tool (Girvetz et al. 2009).

Projected future temperature and precipitation values were downscaled from 16 general circulation models (GCMs) run for a mid- to high-CO₂ emissions scenario (SRES A2) (Nakicenovic et al. 2000). This scenario provided the closest approximation of the current emission trajectories for the 3 scenarios for which all 10 GCMs were run. We chose to explore the range of projections from multiple GCMs and a single scenario because there is more variation in the output of the GCMs than from using the 3 scenarios. We calculated median changes in temperature and precipitation for all 16 models within the ranges of each of the 4 *Martes* species.

American Marten and Fisher

We projected that both the American marten and the fisher will experience warming throughout their ranges by the end of the 21st century (Figs. 1a,c). We projected that average annual temperatures will increase by more than 5° C in far northern and western Alaska and in the area directly south of Hudson Bay. The ensemble of 16 projected future climates showed the least change for the 2 *Martes* species in coastal portions of British Columbia and California, where we projected that temperatures will increase by less than 3° C by the end of the century. It is important to note, however, that these temperatures were the medians of the 16 projections; thus, some of the models project larger, and some smaller, increases in temperature. No models projected decreases in temperatures throughout the species' ranges.

We projected that total annual precipitation will increase throughout most of the ranges of the 2 North American species (Figs. 1b and 1d). Projected increases were largest in the far Northwest and Northeast, where total annual precipitation is projected to increase by >20 cm. In the southern portions of the species' ranges, we projected that total annual precipitation will decrease by 5-20 cm.

Stone Marten and European Pine Marten

For both European species, we projected that temperatures will increase throughout their ranges (Figs. 2a,c). For the stone marten, the greatest increases in temperature were in central Spain, where we projected that average annual temperatures will increase by 4-5° C. For the pine marten, we projected that the greatest increases in temperature will be in the far northeastern part of its range in Finland and northern Sweden. We projected that the smallest changes in temperature for both species will occur in western France, the United Kingdom, and Ireland.

In general, we projected that total annual precipitation will increase in far northern Europe and decrease in central and southern Europe (Figs. 2b,c). Thus, we projected a decrease in precipitation across much of the stone marten's range, and for the pine marten, we projected a decrease across the southern half of its range, and an increase across the northern half. We projected that the stone marten will experience the largest decreases (>20 cm) in total annual precipitation across the western Balkan and Iberian Peninsulas and the largest increases (10-15 cm) at the northern extent of its range. We projected the pine marten to experience increases in precipitation of >15 cm in most of Scandinavia and Scotland.

PROJECTED RANGE SHIFTS

We projected climate-driven changes in the ranges of each of the 4 species using bioclimatic models (Pearson and Dawson 2004). Bioclimatic models, often referred to as climate-envelope

models, are based on correlative relationships between the current distribution of a species and current climate. The models are applied to projected future climate data to estimate the future potential range of the species. These correlative models have their shortcomings. For example, they do not account for behavioral or evolutionary changes, they do not directly model interspecific interactions, they cannot adequately account for future non-analogue climatic conditions, and they assume that the range of the species being modeled is at equilibrium (i.e., not expanding or contracting). Despite these shortcomings, these models provide a useful first approximation of potential changes in habitat conditions under various climate-change scenarios.

We obtained data for building the models from several sources. We derived distribution data for the 2 North American species from digital range maps of their breeding ranges (Patterson et al. 2003). We mapped these data on a 50- by 50-km cell grid, whereby we considered each species to be “present” or “absent” in each grid cell based on whether that cell fell within or outside the mapped range of the species. Because the map of the fisher’s current range that we used to build our model did not include areas where fishers had been extirpated, but have been reintroduced relatively recently, we built a second model for the fisher based on a digitized map of its presumed historical range (Powell 1982). If differences between the fisher’s historical and current ranges are due to extirpation (either directly through trapping or indirectly through habitat loss), building a bioclimatic model based on current distribution will result in an overestimate of the potential impacts of climate change on the fisher’s range. However, differences between current and historical ranges could have resulted from recent climate changes (see Krohn, this volume); consequently, building a model based on historical range and current climate may underestimate the potential impacts of climate change. Consequently, we explored potential climate-driven range shifts for the fisher by using both current and historical

ranges to build our models. We obtained distribution data for the 2 European species from the Global Biodiversity Information Facility data portal (<http://data.gbif.org>), gridded to 50- by 50-km cells. These occurrence data included both museum specimens and observational data; there were >1,000 occurrences for each species.

We built models for the North American species based on recent climate data from the 30-min CRU CL 1.0 (New et al. 1999) and 10-min CRU CL 2.0 data sets (New et al. 2002). We downscaled these data to our 50-km grid and averaged them for a 30-year period from 1961 to 1990. This downscaling involved a topographically informed spatial interpolation. Thus, the downscaled layer takes into account the effects of elevation and aspect on temperature and precipitation patterns. To build the bioclimatic models, we used a set of 37 bioclimatic variables (e.g., evapotranspiration, total annual snowfall) derived from the temperature, precipitation, and sunshine data in the CRU datasets. See Lawler et al. (2009) for complete descriptions of downscaling methods and bioclimatic variables. We derived recent climate data for the European species for the same time period (1960-1990) from the same dataset used to summarize historical changes in climate for the European species (see previous section on Recent Changes in Climate). We based models for the European species on 34 variables including monthly, seasonal, and annual mean temperatures, and total precipitation values. Although we could have used the same global data set and variables for both North American and European *Martes* species, we wanted to take advantage of the more-detailed climate data set available for North America for modeling the American marten and fisher.

We used a 50-km grid to balance the relatively coarse nature of the species distribution data and the need to capture relatively fine-scale climate variation (e.g., the effects of topography). Although the climate datasets do capture the effects of large mountain ranges, they do not

capture finer scale topographic relief. Thus, projections based on the bioclimatic models do not address the relatively fine-scale effects of slope, aspect, and elevation, nor do they capture finer scale effects of climate on potential habitat.

We built bioclimatic models for all species using the approach described in Lawler et al. (2009). We built all models using random-forest predictors (Breiman 2001, Cutler et al. 2007). Random forests are a machine-learning, model-averaging approach based (in our study) on classification trees. Random-forest models been shown to perform better than many other approaches for modeling species distributions (Lawler et al. 2006, Prasad et al. 2006, Cutler et al. 2007). We built the models using 80% of the data, and reserved the remaining 20% for a semi-independent model validation.

For the North American species, we used projected future climate data from 10 different GCMs run for a mid-high (SRES A2) greenhouse-gas emissions scenario. We obtained future climate projections from the World Climate Research Programme's Coupled Model Intercomparison Project phase 3 multi-model archive (http://www-pcmdi.llnl.gov/ipcc/about_ipcc.php). We downscaled projected future temperature anomalies to the North American 50-km grid by spatially interpolating the values for the coarser GCM grid. We added these anomalies to the current climate variables and then recalculated the 37 bioclimatic variables. We then calculated future climate data as a 30-year average for the period 2071-2099. For the European species, we used projected future climates from 16 different GCMs run for the mid-high (SRES A2) greenhouse-gas emissions scenario. We downscaled anomalies from these projections to the same European grid, and added to the current climate data to generate the 34 variables for the period 2071-2099.

American Marten and Fisher

Models for both species accurately predicted their current distributions. The model for the American marten correctly predicted 96% of the test data set that were within the range, and 98% of the test set data that were outside the range. Models built with current and historical ranges for the fisher predicted 91 and 92%, respectively, of the test data set within the range correctly, and both models correctly predicted 99% of the test data set outside of the range. Models for both species projected potential climate-driven range expansions to the north and contractions across much of the southern extent of the ranges (Fig. 3). We projected that both species will lose most of their climatically suitable range in the contiguous U.S. by the end of this century. For the American marten, projected contractions were greatest in the central western U.S. and around the Great Lakes. The largest area of range expansion for the fisher was in the north-central and northeastern parts of its range. For the American marten, Hudson Bay prevented an expansion in the central part of its range, but we projected large expansions to the east and west of the Bay. Models built using both current and historical ranges for the fisher produced similar projected range shifts (Figs. 3b,c).

Stone Marten and European Pine Marten

Models for both stone and pine martens correctly predicted 97 and 97% of presences in the test data set, and 97 and 98% of the absences, respectively. Both models projected potential range contractions across much of Europe (Fig. 4). For the stone marten, there were very few places where all 16 projected future climates resulted in a projected stable range (Fig. 4a). However, there was only moderate agreement among model projections for the contractions projected in most of its range. The areas with the most model agreement for range contractions were in southern Europe, particularly the southern half of Spain. Similarly, although the models projected a large area of potential range expansion for the stone marten (Fig. 4a), there was

relatively little model agreement across most of this zone of potential expansion. The areas with the greatest model agreement for expansions were in southern United Kingdom, Ireland, and Scandinavia.

For the pine marten, a slightly larger but still relatively small portion of the range was projected to be stable under all 16 projected future climates (Fig. 4b). There was relatively high model agreement for range contractions across much of the southwestern and eastern portions of the range and low model agreement for contractions throughout most of the species' range in continental Europe. Projections of future climates resulted in relatively few areas of potential range expansion, and very few areas where there was high model agreement for such expansions.

POTENTIAL CLIMATE IMPACTS ON FISHER HABITAT IN CALIFORNIA

The southernmost fisher populations in North America are in the Sierra Nevada and Klamath Mountains of California (Fig. 5). These 2 populations are believed by many to represent disjunct remnants of a formerly contiguous range in California (e.g., Wisely et al. 2004). Fisher conservation is a major management concern in California, especially in the Sierra Nevada, where lawsuits challenging proposed actions by federal land management agencies in both occupied and unoccupied fisher habitat are common.

In California, fisher home ranges are characterized by forest structural characteristics that are strongly skewed toward mid- to late-seral stands with high canopy cover and large cavity-forming trees that are required for resting and denning (Zielinski et al. 2004b, Yaeger 2005). Oaks, primarily black oak (*Quercus kelloggii*), are a key component of California fisher habitat, particularly in the Sierra Nevada (Zielinski et al. 2004a, Davis et al. 2007). In California, forest-structural conditions associated with fisher occurrence are correlated with areas of complex topography, steep (often north-facing) slopes, and proximity to water, especially in the Sierra

Nevada, where precipitation is lower and summertime drought is more pronounced than in the Klamath Mountains (Zielinski et al. 2004b, Carroll 2005).

Potential climate-change impacts on the fisher and its primary habitat in California have yet to be evaluated quantitatively. Climate change is likely to affect fisher habitat in California by altering species and structural composition directly through changes in climatic conditions and competitive relationships, and indirectly by altering fire and other disturbance regimes. Climate-driven changes in tree-species composition may either decrease or increase the amount of habitat available to fishers for foraging, denning or resting. Climate-driven changes in fire regimes are likely to drive much of the short-term response in vegetation floristics and structure (Flannigan et al. 2000, Dale et al. 2001). If longer or more severe fire seasons result from climate change, the probability of losing local populations of species that are associated with late-seral habitat conditions will increase (McKenzie et al. 2004).

The landscape-scale: GCM-based projections of future fire regimes and vegetation types for fishers in California

In this section, we combine previously published GCM-based model projections of fire regimes and vegetation response in California (Lenihan et al. 2003a,b; 2008) with stand-scale fire and forest-growth modeling outputs to explore potential future climate-driven changes to fisher habitat in California. Lenihan et al. (2008) projected potential future changes in fire regimes and vegetation across California using outputs from 2 different GCMs. The GFDL CM2.1 model (medium climate sensitivity of about 3° C for a doubling of CO₂ above pre-industrial levels) and the NCAR PCM model (lower sensitivity of about 1.8° C for CO₂ doubling) were both run from 1895 to 1995 using observed trends in greenhouse gases, and into the future using the SRES A2 and B1 emission scenarios (IPCC 2007b). Climate outputs from these models were input into

the dynamic global vegetation model MC1, which models changes in vegetation and fire and other ecosystem properties (Lenihan et al. 2003a,b; 2008).

We overlaid outer range boundaries for the 2 California fisher populations onto maps of projected vegetation-type distributions in Lenihan et al. (2008) for the period 2071-2100, summed the number of pixels of each vegetation type occurring within the current population areas, and compared the outcomes to the current (modelled) condition. We also overlaid the fisher range boundaries on maps of projected changes in fire frequency and intensity presented in Lenihan et al. (2003a). The 2003 effort was similar to the 2008 effort, but used different GCMs (Hadley CM2 and an earlier version of NCAR PCM) and did not incorporate the IPCC emissions scenarios (Lenihan et al. 2003a,b).

It is important to note that the Lenihan et al. (2003a,b; 2008) MC1-based modeling efforts were conducted on a 10- by 10-km spatial grid. This is a high resolution for this type of model, but fisher habitat quality depends primarily on vegetation and landscape features that occur at finer spatial scales than 100 km². Thus, the MC1-based results we summarize below represent broad, landscape-scale patterns of hypothesized change whose influence on fisher habitat will be filtered by variability in topography, vegetation, and other factors that occur outside the resolution of the MC1 model. In addition, the fire module in MC1 was calibrated by Lenihan et al. (2003a,b; 2008) to restrict the occurrence of simulated fires to extreme events. They explain that “Large and severe fires account for a very large fraction of the annual area burned... and these events are also... least constrained by heterogeneities in topography and fuels that are poorly represented by relatively coarse-scaled modeling grids” (Lenihan et al. 2003a:1669). Although fires in the California fisher population areas (especially in the southern Sierra Nevada) may have been dominated by smaller fires of low- and mixed-severity effects

historically (and thus poorly represented by the MC1 fire module), fire-exclusion policies result in the immediate suppression of almost 99% of ignitions on National Forest lands in California. Increasing forest fuels and warming climates have led to a situation where uncontrolled fires in the mixed-conifer zone are becoming larger and burning at increasingly severe levels (Miller et al. 2009). We conclude that the MC1 fire module is probably a reasonable representation of future fire activity, at least at the broad scale of application.

Lenihan et al. (2008:S226) projected increases in the annual area burned by wildfire throughout most of California by the end of the 21st century. In the Sierra Nevada fisher population area, annual area burned by wildfire was projected to increase on about 10-15% of the landscape and remain stable on 85-90% of the landscape, depending on the GCM-emissions scenario. Lenihan et al. (2008) projected much greater changes in burned area in the Klamath fisher population area, with increases occurring on 20-27% of the landscape, but decreases occurring on 2-5% of the landscape. In both population areas, the GFDL-A2 scenario (much warmer and drier than today) produced the greatest increases in burned area.

Lenihan et al. (2003a,b) included maps of projected changes in mean fire frequency and intensity under the Hadley CM2 and NCAR PCM GCM scenarios (with no specific emissions assumptions). The Hadley CM2 model projected much higher future precipitation in California, which is now considered unlikely by most climate experts (Cayan et al. 2009). Like most of the current GCMs, the NCAR PCM model used by Lenihan et al. (2003a,b) projected gradual decreases in annual precipitation during the next century, but their temperature projections are among the more optimistic scenarios, with only about 2.4° C warming. We report the NCAR PCM-based outputs here. For the Klamath Mountains fisher population area, Lenihan et al. (2003a,b) projected more frequent fires in about 50% of the landscape, with most of those areas

experiencing decreases of 10-50% in average fire-return intervals (FRIs) (i.e., 10-50% more fires). About 45% of the landscape was projected to have similar fire frequencies to today, and 5% was projected to have decreased fire frequencies. In contrast, in the Sierra Nevada population area, they projected more frequent fires in about 30% of the landscape, with fire frequencies remaining similar to today on most of the remaining landscape. In both population areas, most areas with greatly increased fire frequencies are associated with areas where conifer forest transitions to hardwood-dominated mixed forest and woodland. Projected transitions from woody vegetation to grassland also drive (and are driven by) higher fire frequencies in the Sierra Nevada (Lenihan et al. 2008).

Lenihan et al. (2003a,b) projected that average fire intensities will remain unchanged or decrease in 90% of the Klamath Mountains fisher population area. This is due primarily to widespread transitions from conifer to hardwood-dominated forests and woodlands. In contrast, in the southern Sierra Nevada, they predicted increases in fire intensity in about 35% of the fisher population area and decreases on 15% of the landscape; fire intensities were projected to remain similar to today on about 50% of the landscape. Lenihan et al.'s (2003a,b) projected changes in fire intensity are primarily due to changes in fuels growth due to climatic factors, changes in fire frequencies, and vegetation-type shifts to more or less flammable fuels. For example, transitions from woody vegetation to grassland are accompanied by increased fire frequencies but decreased fire intensities, and a similar pattern occurs where conifer forest transitions to hardwood-dominated vegetation. Most locations projected to remain in the same vegetation type will only experience either moderate or no changes in fire regime.

Interactions between climate and fire generate significant changes in projected vegetation cover in both California fisher population areas (Lenihan et al. 2008; Fig. 6). In the Klamath

Mountains, all of the GCM-emissions scenarios projected losses of >50% in conifer-forest cover by 2100, with increases of about 100% in mixed (hardwood-dominated) forests, and 100-400% in mixed woodlands. Shrubland and grassland cover were projected to change only minimally. In the Sierra Nevada, the different GCMs projected 25-75% losses in conifer forest (Fig. 6). The response of mixed forest depends strongly on the GCM, but mixed woodland was projected to increase in area by at least 40%; overall, the area of hardwood-dominated vegetation was projected to increase by 45-75%. Grassland increases substantially, especially in the drier GFDL scenarios (Fig. 6). In the most extreme (GFDL-A2) scenario for the Sierra Nevada population area, grassland and shrubland cover >50% of the landscape by 2100, and conifer-dominated forest <10%. Note that, except for the last scenario described (GFDL-A2 for the southern Sierra Nevada), all of the simulated vegetation outcomes for both fisher population areas predicted that the overall extent of forested landscape will not change appreciably during the 21st century. The biggest projected change is a transition to hardwood-dominated forest types from conifer-dominated types (Fig. 6). In areas where mixed woodland is predicted to rise substantially in importance, we can expect a decrease in canopy cover within these forested stands.

The stand-scale: simulations of fire effects on forest structure for fishers in California

To explore the potential impacts of projected changes in fire regimes at the landscape scale on fisher habitat at the scale of the forest stand, we simulated the effects of fire regimes with different frequencies and severities on forest structure in the southern Sierra Nevada population area. We used the Fire and Fuels Extension to the Forest Vegetation Simulator (FVS-FFE) (Reinhardt and Crookston 2003) to model fire effects on the structure of late-seral conifer forest in the southern Sierra Nevada. To parameterize the model, we used Forest Inventory and Analysis (FIA) plots sampled on the Sierra and Sequoia National Forests. We used the fisher

resting-habitat-quality index developed by Zielinski et al. (2006) to rank FIA plots on both National Forests, and chose the 40 plots with the best fisher habitat. Most of the plots were in the mixed-conifer type, and many had a significant component of oak and other hardwoods.

We used FVS simulations to grow trees in each plot for 90 years, beginning in 2010 and ending in 2100, and ran fire simulations for 3 different fire-weather scenarios between June 15 and September 15 (high = 97th percentile weather; moderate = 80th percentile weather; low = 10th percentile weather [this essentially corresponds to a prescribed-fire scenario]) at FRIs of 10, 20, 30, 50, and 100 years. We assessed variables at 10 decadal time steps. We derived fire-weather scenarios from the Shaver Lake “RAWS” climate station (elevation 1,710 m), which is in the middle of the elevational and latitudinal range of the fisher in the Sierra Nevada, using the fire-weather ranking system in the Fire Family Plus program (Main et al. 1990). As a control, we also simulated the same stands without fire. We tracked the following variables, which are correlated with occupied fisher habitat in California and elsewhere (Powell 1993, Zielinski et al. 2004b, a, Zielinski et al. 2006): tree canopy cover; number of large trees (dbh ≥ 76 cm) per acre, number of hardwood trees per acre, number of large snags (dbh ≥ 76 cm) per acre, and number of down logs ≥ 30 cm diameter per acre. We report results from the following 7 fire-regime scenarios: control (no fire); 20-year moderate and low severities; 50-year high and moderate severities; and 100-year high and moderate severities. We report these scenarios for the following reasons: (1) because moister, mixed-conifer stands in the pre-European era in the Sierra Nevada are thought to have burned at mean FRIs of 10-20 years, primarily at low and moderate severities (Sugihara et al. 2006, Stephens et al. 2007); (2) because of historical fire-suppression policies, most areas in the Sierra Nevada have not burned in the last century, hence the 100-year FRI; and (3) the 50-year FRI represents a 50% increase in fire, which is the upper

bound of likely increases in fire frequency for most places in the California fisher population areas projected to experience more fire by the end of the century (Lenihan et al. 2003a,b; 2008).

We began the FVS-FFE simulations with a mean of 26 large trees per hectare, but different fire-regime scenarios produced highly variable responses by the end of the century (Fig. 7a). At the end of the 90-year period, the mean number of large trees per hectare was highest in the control plots, followed by the 100-year moderate-severity scenario and the 20-year low-severity scenario. Taking the average number of large trees in the simulated plots over the entire time period (i.e., the mean of the 10 decadal time steps), the same 3 scenarios supported the most large trees, whereas the 50-year high, 100-year high, and 20-year moderate scenarios supported the fewest large trees per hectare (Table 1). For all hardwoods ≥ 6 cm dbh, final (i.e., in 2100) and overall mean hardwood tree densities were not significantly different among scenarios, but the mean density of large hardwoods (≥ 20 cm dbh) was about twice as high in the control and 20-year low scenarios as in any of the other scenarios ($F = 13.37$, $P < 0.0001$). Tree canopy cover from all size classes (including seedlings and saplings) was highest in the 100-year and 50-year high-severity scenarios, both at the end of the scenario and as an average of the entire simulation period. The lowest canopy cover was in the 2 20-year fire scenarios (Table 1).

By the end of the 21st century, the number of large snags per hectare was highest in the 2 20-year scenarios and in the 50-year moderate-severity scenario. The lowest number of large snags was in the 100-year high-severity scenario (Fig. 7b). When averaged across the simulation period, the highest large-snag densities were in the 20-year moderate-severity simulation, although they were statistically equivalent to the 20-year low, both of the 50-year, and the 100-year high scenarios (Table 1). The lowest large-snag density occurred in the control plots. When averaged across the simulation period, coarse woody debris was not statistically different

between fire regimes (Table 1), but at the end of the simulation, the highest number of down logs was in the 50-year moderate-severity scenario, and the lowest number was in the 20-year moderate-severity scenario.

We also compared forest structure in the low fire-severity scenarios versus the high-severity scenarios for each FRI class (Fig. 8). The densities of large trees and hardwood trees decreased by 50-75% as fire severity increased, but the density of large snags increased as fire severity increased. For the 10- and 20-year scenarios, canopy cover and coarse woody debris both decreased as fire severity increased, but both variables increased with severity for the 50- and 100-year scenarios, although canopy cover increases were entirely due to small- and medium-sized trees; large trees were almost entirely absent from the high-severity stands. Because 50- and 100-year FRIs rarely if ever burn at low fire-weather conditions, we also compared moderate- and high-severity scenarios for both FRIs. Patterns were similar to Figure 8, except for coarse woody debris, which reversed direction and decreased by 16.6% from the moderate- to high-severity scenarios.

Management implications for fishers in California

The Lenihan et al. (2003a,b; 2008) models suggested that both fire frequency and annual burned area are likely to increase in substantial portions of both fisher population areas during the next century. This generally corroborates findings from other modeling efforts (Miller and Urban 1999, Flannigan et al. 2000, Hayhoe et al. 2004) and extends increasing trends in fire frequency and size for both the Sierra Nevada and Klamath Mountains (Miller et al. 2009; Miller et al., in review). If these trends continue, fisher habitat will be affected. Our stand-scale modeling effort sought to predict what may happen to key fisher habitat attributes under different future fire scenarios. These results showed that fires occurring only rarely (every 50-100 years) under

extreme conditions (i.e., a continuation of current and projected trends) generate high densities of snags and coarse woody debris, but substantially reduce the number of large conifer and hardwood trees, and maintain canopy-cover values only through the recruitment of dense stands of smaller trees (Figs. 7-8, Table 1). In general, we found that shorter FRIs under low and moderate fire-weather conditions were best able to balance the resilience of forests with the creation of legacy forest structures, such as snags and down logs.

There is substantial controversy surrounding current and future management of fisher habitat in California, especially in the critically small Sierra Nevada population area (Spencer et al. 2008). There is general agreement that fire should be reintroduced as a key ecosystem process in the Sierra Nevada, but disagreement as to whether pre-fire fuels treatment is required to protect old-forest habitats. We agree with Spencer et al. (2008) that current and predicted future trends in fire activity warrant fuel-reduction treatments in high fire-risk areas to reduce the probability of losing fisher habitat to fire. At the same time, we also believe that a comprehensive review of fire-management policies should be undertaken throughout the Sierra Nevada. The strong increase in fire size and severity seen in Sierra Nevada mixed-conifer forests during the last quarter century is tied to increasing forest fuels and warming climates (Miller et al. 2009), but it is also linked to current fire-management practices, which extinguish nearly all fires burning in moderate weather conditions, except those on National Park lands. These are precisely the fires that are most likely to both preserve and create habitat for old-forest associates like the fisher. More than 30 years of let-burn policies in Yosemite and Sequoia-Kings Canyon National Parks have returned many areas in these Parks to nearly pre-suppression era conditions (Collins and Stephens 2007). Even moderate relaxation of fire-suppression policies and practices outside the parks (e.g., to allow for some naturally ignited fires under

moderate weather conditions, especially after forest fuels were reduced in high-risk areas) would be a significant step toward sustaining naturally functioning forests and the wildlife they support.

CONCLUSIONS

Our bioclimatic models indicate that climate change will likely result in relatively large changes in the distribution of both North American and European *Martes* species. In North America, multiple climate-change scenarios consistently projected northward range shifts for both the American marten and fisher. In Europe, greater variability in climate projections resulted in much less agreement about the nature of range shifts, but suggested the potential for large range contractions for both species, and relatively small range expansions for the pine marten.

These projected changes have potential implications for the management of several populations in each of the 4 species. There are 7 states and provinces in which American martens are protected: California, Nevada, Newfoundland, New Hampshire, Nova Scotia, South Dakota and Wisconsin (Proulx et al. 2004:52-54). Populations in South Dakota, Wisconsin, New Hampshire, and Nova Scotia are all likely to experience shifts in climate that will make those areas less suitable for martens due to increased temperatures and/or loss of snowpack. Although the 2 most endangered populations (the subspecies *M. a. atrata* in Newfoundland, and *M. a. humboldtensis* in north-coastal California) are not projected to experience a complete loss of suitable climates, they will likely experience warmer temperatures. Warmer temperatures and decreases in snowpack may have detrimental effects on the Newfoundland subspecies; however, because the Humboldt marten does not occur in areas where snowpacks accumulate, it may experience fewer negative effects of climate change. Projected potential range contractions in the southeastern portion of the fisher's range in California raises the question of how much effort should be put into reintroductions in that region, or maintaining reintroduced populations in West

Virginia, Pennsylvania, or New York, should they begin to decline. We are not suggesting that additional reintroductions are unwarranted. However, range-shift projections can be useful when deciding among areas for reintroductions or between putting effort into maintaining a population in an area that is projected to remain climatically suitable vs. reintroducing fishers into an area that is projected to become climatically unsuitable.

Given that models for the 2 European martens did not include distribution data for the eastern portions of the ranges, we are more cautious about the management implications of projected range shifts. Nonetheless, these models can be used to anticipate potential future population declines, particularly in populations that are already at risk. For example, protected populations of the stone marten in Albania, Bulgaria, Hungary, Portugal, and Spain are likely to experience increased risks of extirpation due to increasing temperatures.

One of the largest shortcomings of bioclimatic models, such as those reported here, is their correlative nature. These models do not address many of the mechanisms that affect species distributions directly. However, mechanistic models applied within the fisher's current range in California provide some support for range contractions projected by the bioclimatic models. The increase in mixed-evergreen forest projected for both the Klamath and southern Sierra Nevada fisher population areas suggests that floristic conditions for fisher survival may be enhanced by climate warming, as long as annual precipitation remains near or above current levels, and as long as direct temperature (or other) effects on metabolic rates for the fisher and its prey do not result in significant range shifts upward in elevation. However, the drier climate-change scenario resulted in the conversion of large expanses of forested area to grasslands and shrublands. Furthermore, although our simulations indicate that projected increases in fire frequency, area, and intensity will likely lead to increases in large snags and down logs, such

increased fire activity will likely also lead to decreases in the density of large trees and the canopy cover they provide. Given that overstory cover and the density of large trees are among the factors most closely correlated with fisher occurrence in California (Powell 1993, Zielinski et al. 2004a,b), the net result of these simulated changes in forest structure may ultimately be a decrease in fisher habitat.

Other studies have come to similar conclusions about the potential effects of future climate change on the distribution and habitat of at least 2 of the 4 species we discuss here. Based on historical trends, Krohn (this volume), concluded that increased warming will likely lead to further contractions at the southern edge and expansions at the northern edge of the ranges of both the American marten and fisher in the eastern U.S. Additionally, he concluded that the fisher will likely continue to be distributed further south than the marten, which is a pattern we also found in our model projections. Carroll (2007) projected a 40% decline in American marten populations in the far eastern portion of their range as a result of reduced snowpack resulting from projected changes in climate. Burns et al. (2003) used regression models of vegetation associations of animal species and climate-change effects on vegetation in a subset of U.S. National Parks to predict mammalian species turnover by the end of the 21st century. They found that the fisher was one of the most climate-sensitive carnivores and predicted its loss from both of the National Parks in California where it occurs today. Miller et al. (2009) found that trends in both fire severity and size since the early 1980's in the Sierra Nevada were strongly positive, particularly in those forest types that support old-forest associated species like the fisher. Miller and Urban (1999) conducted a long-term (500-800 years) simulation for the Sierra Nevada and found that fires were projected to be more frequent under future climate, and that forests at lower elevations would be replaced by grasslands and more-open woodlands.

Flannigan et al. (2000) projected that seasonal fire-severity ratings would increase by 10-30% by the middle of the 21st century in most of the areas occupied by fishers. These results are similar to the climate-, fire- and vegetation-change projections reported by Lenihan et al. (2003a,b; 2008).

Although our models capture some of the potential effects of climate change on American martens and fishers, there are several other ways in which climate change will likely influence these species. For example, temperature extremes (which were not captured in any of our modeling efforts) may be more important than mean values in driving species distributions. Hayhoe et al. (2004) found that the probability of extreme heat events in California will undergo a marked increase as temperatures rise. They estimated that there will be 22 more days with maximum temperatures $>32^{\circ}\text{C}$ by the year 2100. Although extreme high temperatures may have direct effects on fishers, they may also indirectly affect fishers through their effects on prey species. Likewise, changes in fire frequency and forest structure will also influence prey availability.

Climate change is also likely to result in a number of other complex and largely unpredictable effects on *Martes* species. For example, the complex relationships between rising temperatures and drought, water stress, insect and disease occurrence, and fire appear to be already driving rapid ecosystem response to climate change in Western forests (Dale et al. 2001, Breshears et al. 2005). Such feedback effects among multiple disturbances are thought to represent causal factors for recent large-scale geographic shifts in the distributions of ponderosa (*Pinus ponderosa*) and piñon (*P. edulis*) pines in the southwestern U.S. (Allen and Breshears 1998). In many cases, insect- or disease-caused mortality among conifers may benefit fishers by creating resting, denning, and foraging habitat. However, large inputs of standing and down

dead wood, such as occurs during pine beetle (*Dendroctonus* spp.) outbreaks, may also increase the probability of stand-replacing fires and the resulting loss of critical habitat structures (Shaffer and Laudenslayer 2006, USFWS 2006).

There are, of course, several other factors that neither our broad- or finer scale bioclimatic models take into account. For example, human land use, habitat alteration, and both predator-prey and competitive relationships (among other things) will likely interact with climate change in complex ways. An example of an unforeseen outcome is the recent discovery that pine martens are rapidly expanding into agricultural areas in southern Europe and displacing stone martens, which are competitively subordinate and usually occupy lower quality habitat (e.g., urban and agricultural areas) in areas where the 2 species are sympatric (Balestrieri et al. 2009). Another example of a more nuanced effect of climate change is the potential for reductions in snowpack to alter competitive relationships between martens and fishers. Snow has the potential to mitigate competitive interactions between the species, because martens have a higher foot-loading than fishers (which increases their energetic efficiency) and, unlike fishers, are capable of hunting subniveally (Krohn et al. 1995, 1997, 2005).

Not surprisingly, our results suggest that populations of *Martes* that occur at more southerly latitudes and at lower elevations will be most affected as temperatures continue to rise. However, as our finer scale modeling for the fisher revealed, future climate-change impacts are likely to be more complex. As discussed above, both the broad- and finer scale models presented here can be used to guide management actions at multiple spatial scales. Nonetheless, all models are imperfect representations of reality. Given that future trends can never be projected perfectly, we recommend that those charged with managing *Martes* populations and their habitats implement a variety of management practices that can be monitored and assessed in an

experimental fashion, and apply lessons learned in an adaptive framework. Climate change will undoubtedly challenge our ability to manage and sustain populations of many species. It is our hope that analyses such as those presented here, coupled with adaptive-management approaches and flexible planning frameworks, will help managers and planners meet that challenge.

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Table 1. Mean values for forest-stand variables, averaged across the 10 decadal time steps of the simulation. Each column represents a different fire scenario, including return interval and level of severity. Values with different letters are significantly different among fire scenarios at $P \leq 0.05$ (1-way ANOVA, Tukey HSD).

Variable	Fire scenarios						
	Control	20yr_mod	20yr_low	50yr_high	50yr_mod	100yr_high	100yr_mod
Large trees/ha	33.0c	11.5a	26.3bc	8.7a	20.7b	12.5a	25.2b
Canopy cover (%)	85.9b	69.7a	78.1ab	92.6bc	77.6ab	96.8c	88.4ab
Large snags/ha	8.6a	16.2c	12.2abc	15.6bc	13.7abc	13.0abc	10.5ab
Coarse woody debris (large down logs/ha)	64.0	63.6	64.5	79.4	75.3	85.6	70.8

FIGURE CAPTIONS

Figure 1. Projected changes in temperature (a and c) and precipitation (b and d) for the American marten (a and b) and fisher (c and d). Changes are the differences between climate averaged over a recent 30-year period (1970-1999) and projected climate averaged over a future 30-year period (2070-2099) and are the median of projected climates from 16 different general circulation models (GCMs). Geographic ranges for both species are based on digital range maps in Patterson et al. (2003).

Figure 2. Projected changes in temperature (a and c) and precipitation (b and d) for the stone marten (a and b) and European pine marten (c and d). Changes are the differences between climate averaged over a recent 30-year period (1970-1999) and projected climate averaged over a future 30-year period (2070-2099) and are the median of projected climates from 16 different general circulation models (GCMs).

Figure 3. Projected climate-induced range shifts for the (a) American marten and (b) fisher based on current and (c) historical ranges. Areas of potential range expansion and contraction (the darker shades of gray) represent areas where at least 1/10 projected future climates resulted in a range expansion or contraction. Projections are for an averaged period from 2071-2099. Geographic ranges for both species are based on digital range maps in Patterson et al. (2003).

Figure 4. Projected climate-induced range shifts for the (a) stone marten and (b) European pine marten. Areas of potential range expansion and contraction (the darker shades of gray) represent areas where at least 1/16 projected future climates resulted in a range expansion or contraction. Projections are for an averaged period from 2071-2099.

Figure 5. Locations of the 2 fisher population areas in California.

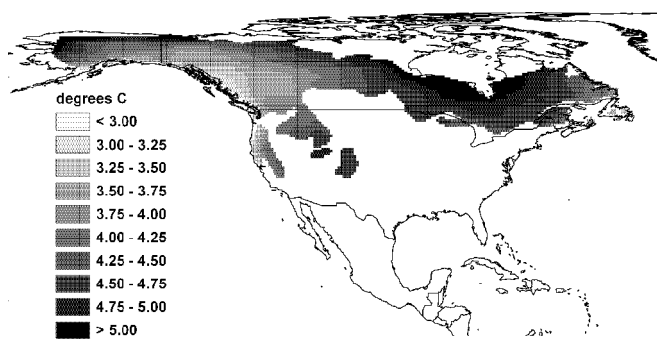
Figure 6. Current (mean during 1961-1990) and predicted future (mean during 2071-2100) projected vegetation types for (A) Klamath Mountains and (B) southern Sierra Nevada fisher populations under 3 future climate-emissions scenarios. Data represent the percent of landscape within each vegetation type. Evergreen conifer forest includes montane and subalpine forests; mixed types are dominated by hardwood species. The PCM-A2 scenario is moderately warmer than today but with similar precipitation; GFDL-B1 is moderately warmer than today but with less precipitation; GFDL-A2 is much warmer than today and much drier. See Lenihan et al. (2008) for more information on these climate-emissions scenarios. Data from Lenihan et al. (2008).

Figure 7. Outputs from FVS-FFE fire and forest-growth simulations for 2 key fisher habitat variables in the Sierra Nevada of California: (A) number of large trees (≥ 76 cm dbh) per hectare, and (B) number of large snags per hectare. See text for details.

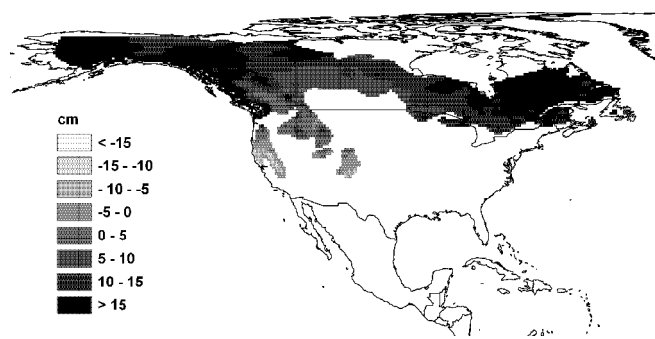
Figure 8. The effects of changing fire severity from low to high on key fisher habitat variables in the Sierra Nevada of California, for 5 fire-frequency classes, measured as

percent change. Data from FVS-FFE fire and forest-growth simulations. See text for details.

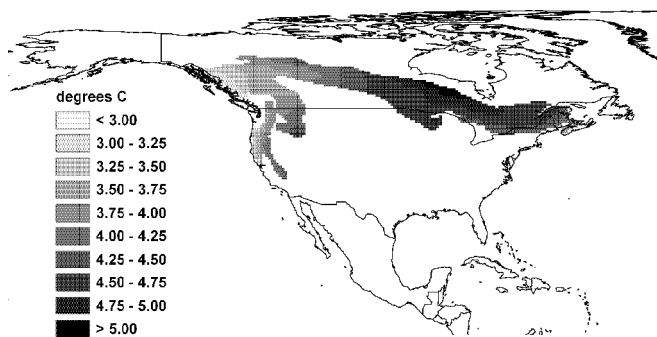
A



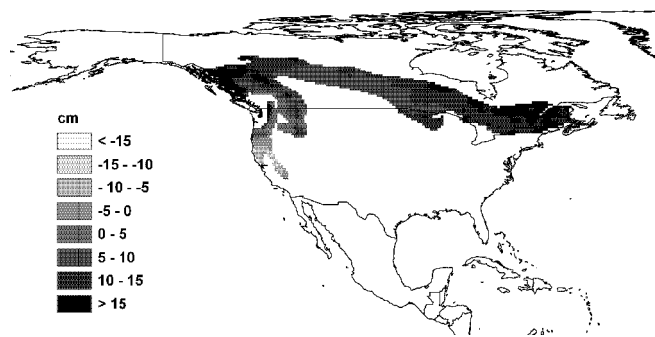
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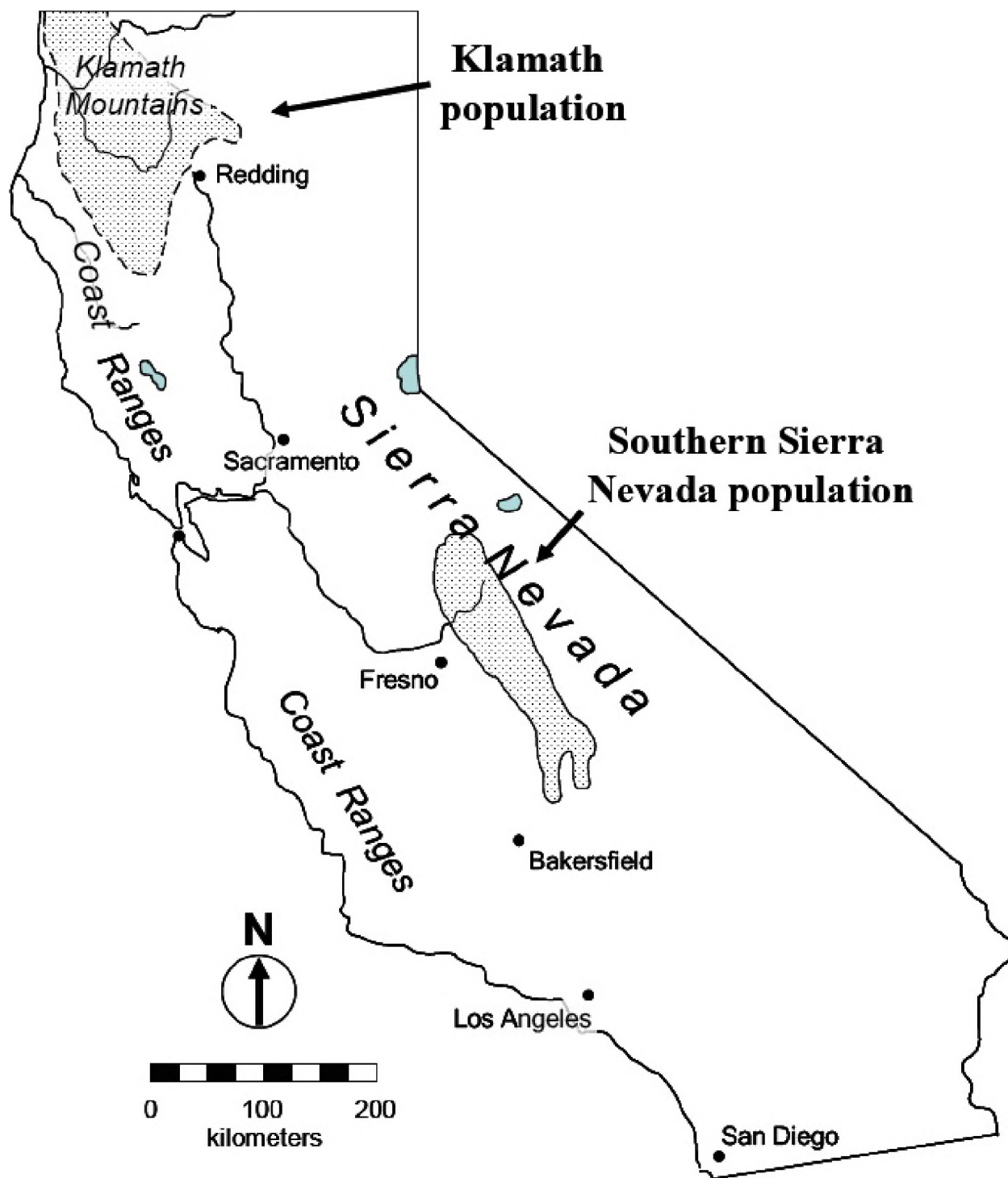


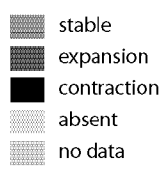
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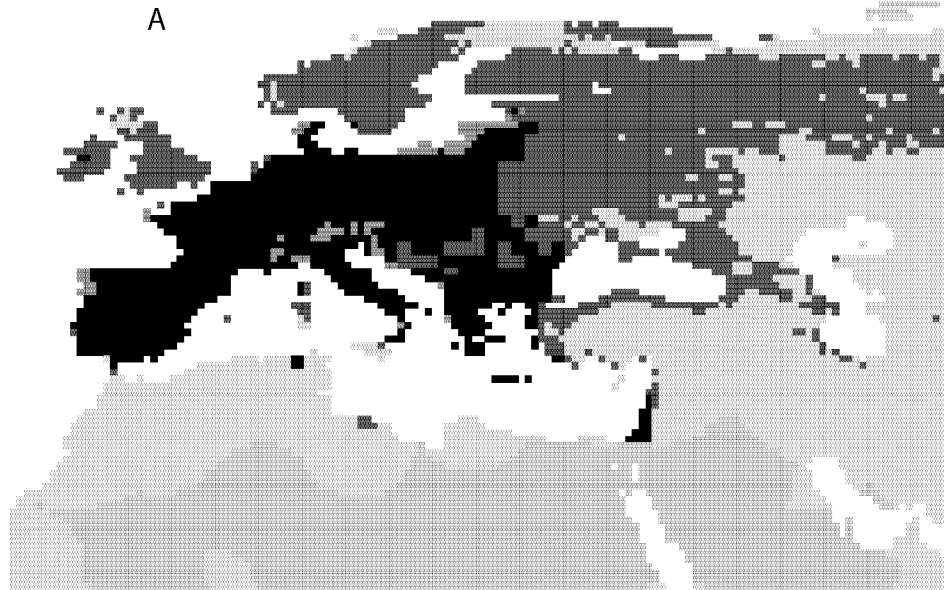
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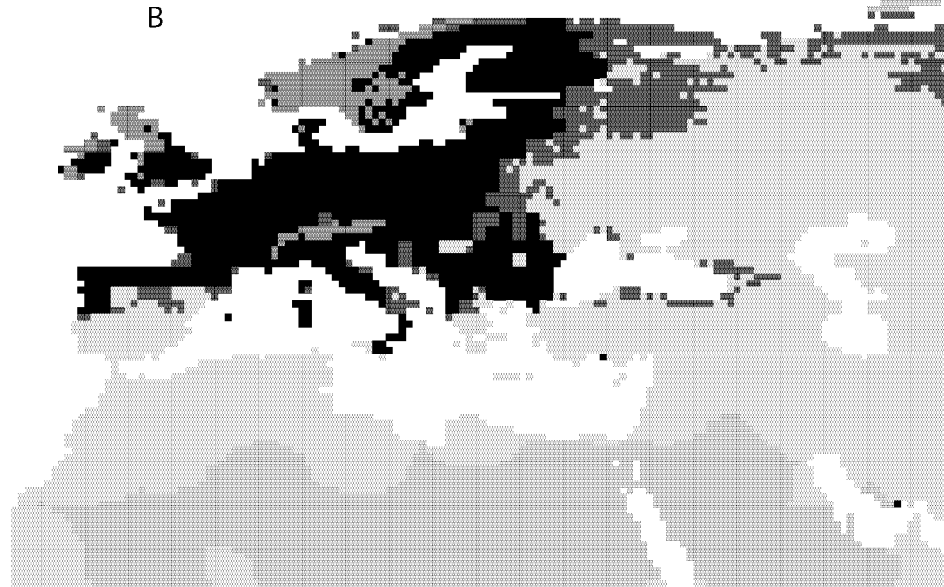


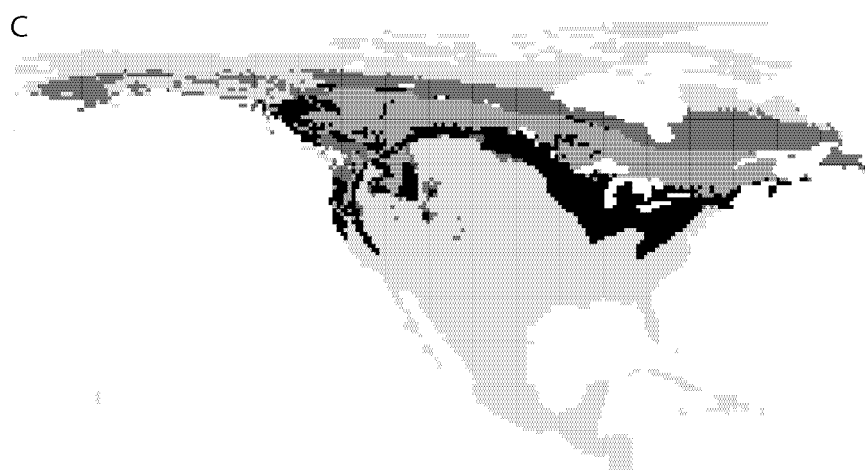
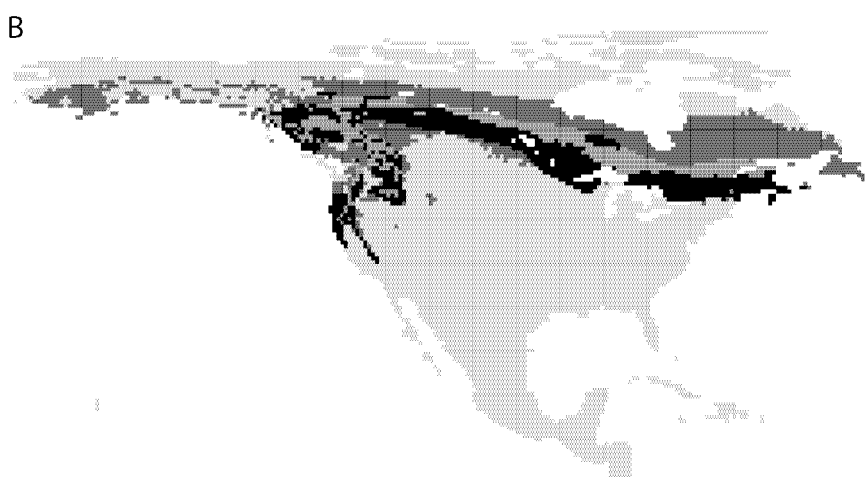
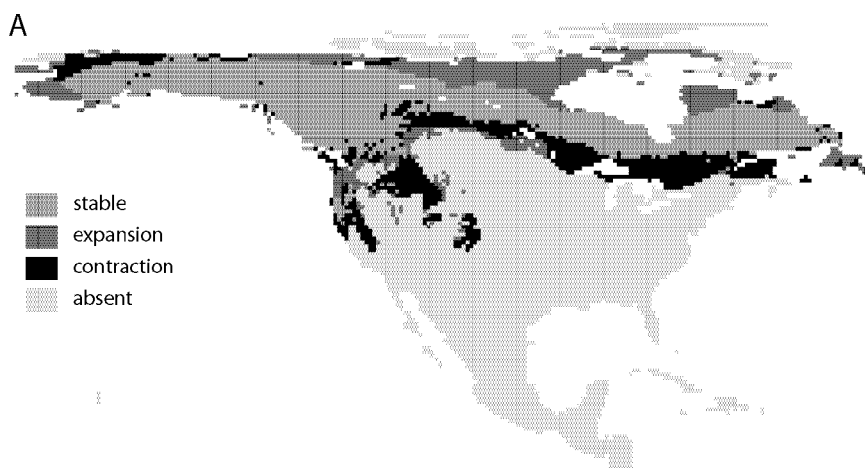


A

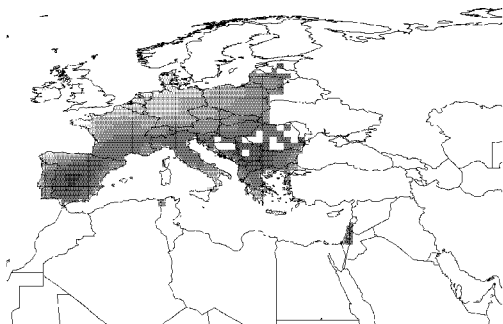
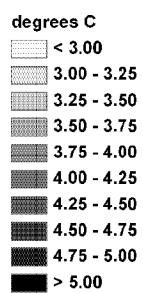


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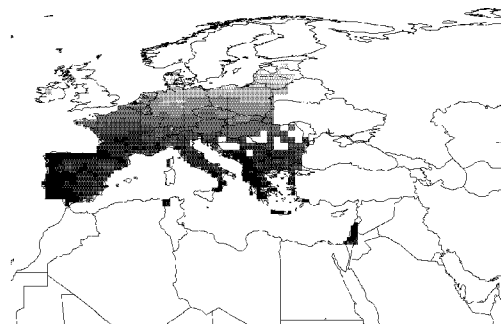
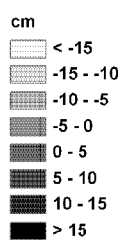




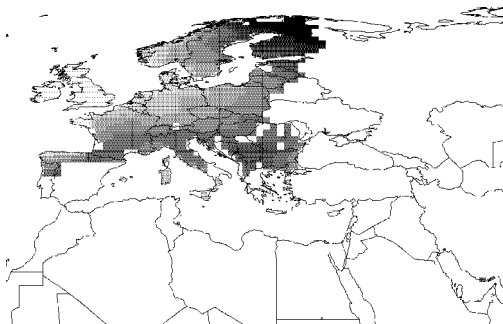
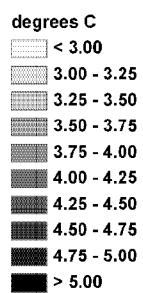
A



B



C



D

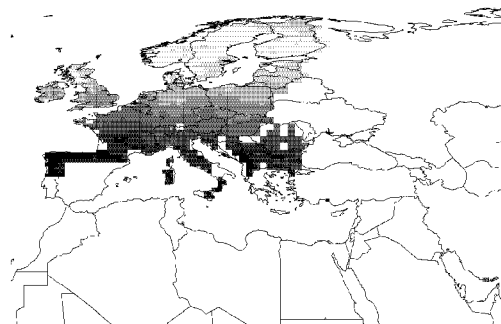
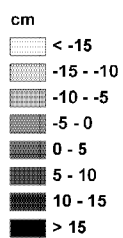


Fig. 6

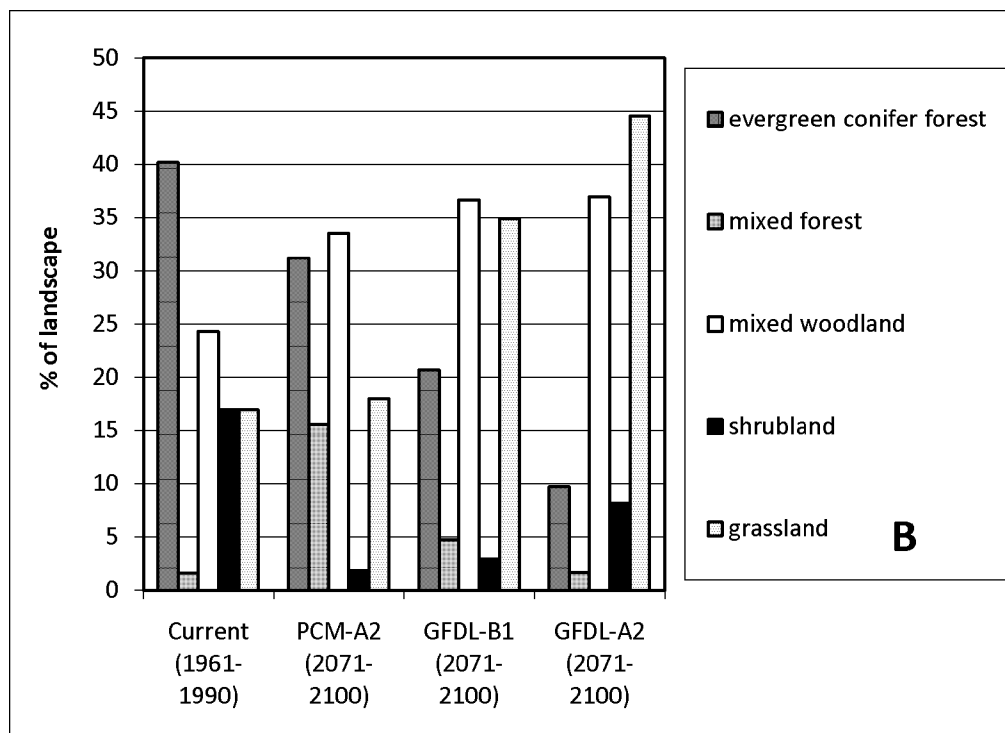
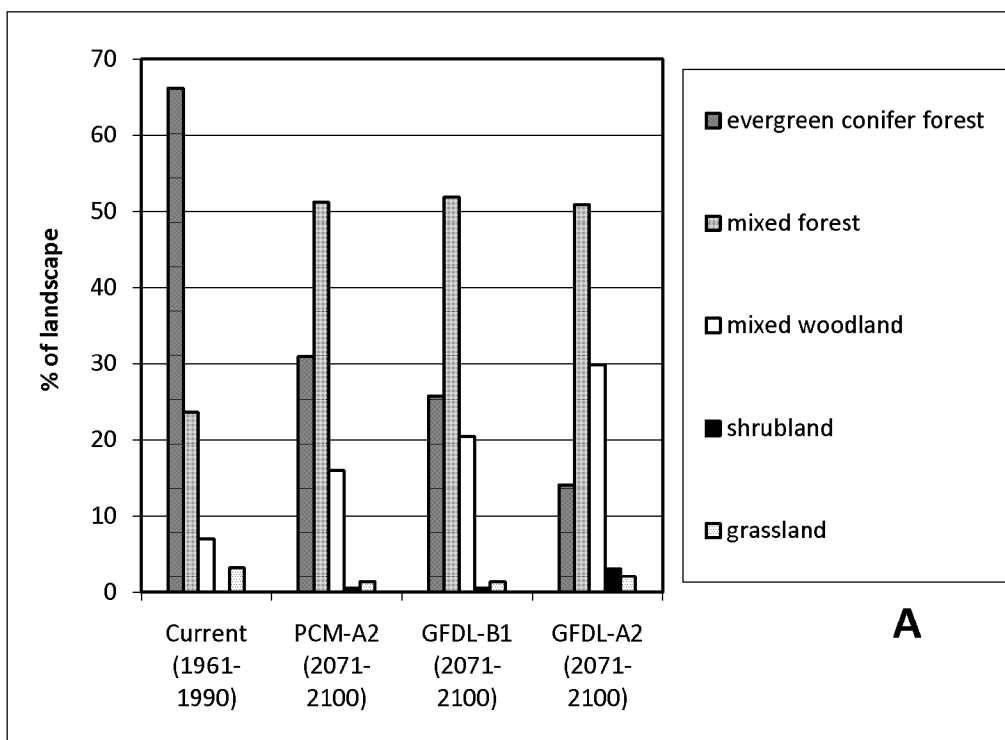


Fig. 7



Fig. 8

