Using occupancy and population models to assess habitat conservation opportunities for an isolated carnivore population

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ABSTRACT

An isolated population of the fisher (*Martes pennanti*) in the southern Sierra Nevada, California, is threatened by small size and habitat alteration from wildfires, fuels management, and other factors. We assessed the population's status and conservation options for its habitat using a spatially explicit population model coupled with a fisher probability of occurrence model. The fisher occurrence model was selected from a family of generalized additive models (GAM) generated using numerous environmental variables and fisher detection–nondetection data collected at 228 survey arrays sampled repeatedly during 2002–2006. The selected GAM accounted for 69% of the Akaike weight using total above-ground biomass of trees, latitude-adjusted elevation, and annual precipitation averaged over a 5 km^2 moving window. We estimated equilibrium population sizes (or carrying capacities) within currently occupied areas, and identified likely population source, sink, and expansion areas, by simulating population processes for 20 years using different demographic rates, dispersal distances, and territory sizes. The population model assumed that demographic parameters of fishers scale in proportion to habitat quality as indexed by the calculated probability of fisher occurrence. Based on the most defensible range of parameter values, we estimate fisher carrying capacity at ~125–250 adults in currently occupied areas. Population expansion into potential habitat in and north of Yosemite National Park has potential to increase population size, but this potential for expansion is predicted to be highly sensitive to mortality rates, which may be elevated in the northern portion of the occupied range by human influences, including roadkill and diseases carried by domestic cats and dogs.

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1. Introduction

The fisher (*Martes pennanti*) is a large member of the weasel family associated with dense, structurally complex, low- to mid-elevation forests in North America (Powell and Zielinski, 1994; Buskirk and Zielinski, 2003; Powell et al., 2003). Remaining populations in the western US are small, disconnected from one another, and threatened by habitat modification and fragmentation (Powell and Zielinski, 1994; Aubry and Lewis, 2003; Zielinski et al., 2005). The Pacific coast population is a candidate for listing under the US Endangered Species Act (ESA), and populations in California are candidates for listing under the California ESA.

Fishers were apparently eliminated from the central and northern Sierra Nevada, California, during the 20th century due to trapping, logging, and other habitat modifications (Zielinski et al., 1995, 2005). This isolated a population in the southern Sierra Nevada, south from the western edge of Yosemite National Park to the Greenhorn Mountains and Kern Plateau (Zielinski et al., 2005). Forests in the region are experiencing increasing risks of large, stand-replacing wildfires due to previous forest management actions (e.g., fire suppression, logging; Agee and Skinner, 2005), climate change (Westerling et al., 2006), and increased ignition rates due to humans (Syphard et al., 2007). However, management actions intended to reduce fire risks (e.g., forest thinning, prescribed fire) have been highly controversial, in part because fishers tend to select the densest forests as resting habitat (Zielinski et al., 2004a).

In 2005, disagreements over proposed changes to forest and fuels management actions by the USDA Forest Service (2004) prompted a coalition of conservation groups to file a successful lawsuit (Sierra Nevada Forest Protection Campaign et al., versus

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Mark Rey et al., 2005) challenging the changes, which included more aggressive forest thinning, increased harvest of large trees to finance the non-commercial thinning, and decreased protections for fishers and other sensitive species. In the context of this conflict, we were asked to perform an independent assessment of the status of the southern Sierra Nevada fisher population, an evaluation of the relative cumulative effects of fires and fuels management actions on the population, and habitat management approaches to help sustain the population. The analytical process was purposely transparent and responsive to input and guidance from stakeholders on all sides of the conflict – including forest managers, conservationists, scientists, and timber industry representatives – in attempt to ensure all parties agreed with the goals, assumptions, and procedures used in the assessment.

This paper presents results of simulation models we used to assess the status of the southern Sierra Nevada fisher population and to investigate opportunities and constraints for increasing the population's size and distribution via conservation and management actions. To accomplish these goals, we coupled a spatially explicit resource selection model with a spatially explicit population model. We used simulations and sensitivity analyses to estimate the population's potential carrying capacity under various assumptions and to identify potential population source, sink, and expansion areas. Results are being used as hypotheses to test with field research; they also provide spatially explicit information concerning where vegetation management actions may most benefit fishers.

2. Methods

We modeled fisher probability of occurrence at the home-range scale using generalized additive models (GAM) and population dynamics using the spatially explicit population model PATCH (Schumaker, 1998). In coupling these models, we assumed that fisher probability of occurrence strongly correlates with habitat value, and hence fitness, as reflected in differences in births and deaths averaged over time. The ability to scale demographic rates with GIS-predicted habitat value in this manner is a major strength of using spatially explicit population models like PATCH to evaluate conservation issues at the landscape or population scale (Schumaker, 1998; Carroll, 2006). It allowed us to vary model assumptions and parameter values to evaluate their likely effects on the population's size, distribution, and dynamics, and to identify potential population source, sink, and expansion areas.

2.1. Study area

The study area comprises 2,336,171 ha, including all known occupied fisher habitat in the southern Sierra Nevada plus potential, unoccupied habitat that may be important to sustaining or expanding the population, or that may contribute to fires that burn into fisher habitat. The study area includes substantial portions of three national forests (Sierra, Sequoia, and Stanislaus NF) and two national parks (Yosemite and Sequoia–Kings Canyon NP) plus surrounding private and tribal land. The area consists of steep and rugged terrain, from about 30–4400 m elevation, mostly west of the Sierra Nevada crest. Vegetation ranges from chaparral and oak woodlands at lower elevations, to mixed coniferous (pine and fir) forests in middle elevations, to subalpine and alpine communities at upper elevations. Due to California's Mediterranean climate, most precipitation falls as winter rain (at lower elevations) or snow (at higher elevations).

The northern end of the fisher population is in the westernmost portion of Yosemite NP. Fisher were rare to uncommon in the Park in the early 20th Century, when they were affected by commercial trapping, predator control, and logging both inside and outside the Park. Although trapping, predator control, and logging were discontinued in the Park in the 1920s and 1930s, the population apparently has not increased and is currently considered rare in the Park (Chow, 2009). Verified fisher observations since the early 1990s are few and almost exclusively within a narrow elevation band on the western edge of the Park, south of the Merced River Valley (also known as Yosemite Valley) (Chow, 2009).

2.2. Fisher probability of occurrence model

We modeled fisher probability of occurrence using GAM (calculated using the MCGV package version 1.3-30 for R version 2.70) applied to a wide array of environmental variables and systematically collected fisher detection–nondetection monitoring data (Truex and Seels, 2006; USDA, 2006). The monitoring surveys use fixed arrays co-located with Forest Inventory and Assessment (FIA) plots (Zielinski et al., 2006) within the three national forests (NF). The arrays are sufficiently spaced (~5 km apart) to represent independent samples of detected fishers. Each array consists of a central track station surrounded by five track stations positioned ~500 m from the central station at 72° intervals to form a pentagonal sample unit. Tracks were collected from each array every 2 days during a 10-day survey period, for five sample visits per survey. The probability (P) of a single survey at an array detecting a fisher if one is present is estimated to be 0.922 based on a per visit probability of detection (p) of 0.40 and v = 5 visits, using the equation $P = 1 − (1 − p)^v$ (Royle et al., 2008, p. 300). Each array is generally surveyed every other year between June and September. Most arrays were sampled between two and four times from 2002 to 2006.

Although there are 276 total arrays within the study area, we only used monitoring results from south of the Merced River (N = 228) to build occupancy models. Fishers have not been detected north of the Merced by the regional monitoring program or other systematic surveys, despite apparently suitable habitat there (although there are occasional unverified sightings and tracks north of the Merced but south of the Tuolumne River; L. Chow, personal communication). Absence of fishers north of the Merced could be due to historical extirpation and inadequate emigration from occupied areas, rather than lack of suitable habitat conditions (Jordan, 2007; Barrett, personal communications). Therefore, detection–nondetection data south of the Merced were used to create the GAM models, and results were projected north of the Merced to predict habitat potential.

We defined two different fisher response variables from the survey data for model building and testing: (1) MAPE (short for *MArtes PEnnanti*) includes all survey arrays south of the Merced (N = 228) regardless of the number of sample years or fisher detections. Arrays with at least one detection (in any year) were classified as presence points; arrays with no detections across all years were classified as absence points. (2) MAPE2 (N = 169) omits any arrays that were sampled only once, or that were sampled repeatedly but with no more than one detection. Thus, presence points are defined in MAPE2 as those yielding detections in at least two survey years, and absence is defined as points sampled at least twice but with zero detections. We hypothesized that models built using MAPE2 as the fisher response variable may better discriminate locations that are persistently or reliably occupied by fishers from those that may be intermittently or transiently occupied, and thus that MAPE2 models should more strongly reflect habitat quality (and hence fitness) than MAPE models.

We created candidate GAM models using different combinations of potential predictor variables derived from Geographic Information System (GIS) data layers at 1-ha resolution (Table 1). Variable combinations were based on existing fisher occupancy

Table 1
Potential predictor variables derived from GIS layers for use in fisher occupancy models. Variables were calculated as proportions or means across all 1 ha grid cells within a 5 km² moving window.

Cover Type (EVEG)

CON	Proportion of cells in cover types dominated by conifers
PHDWD	Proportion of cells in cover types dominated or co-dominated by hardwood trees
HC_RATIO	Ratio of area in cover types dominated by hardwoods to cover types dominated by conifers
TS_RATIO	Ratio of area in cover types dominated by trees to cover types dominated by shrubs
SHRUB	Proportion of cells in cover types dominated by shrubs
WTM	Proportion of cells with cover type = wet meadow
FORTYPE	Proportion of cells with cover type = Montane Hardwood-Conifer, Montane Hardwood, Ponderosa Pine, Douglas Fir, Sierran Mixed Conifer, Jeffrey Pine, White Fir, Aspen, or Eastside Pine

California Wildlife Habitat Relationship (CWHR) Ratings

CWHR	Average fisher habitat value rating from the California Wildlife Habitat Relationships (CWHR) model for fishers (arithmetic mean of suitability ratings for reproductive, feeding, and cover ratings) * 100
CWHR2	Same as previous but excluding red fir, lodgepole pine, subalpine conifer, and montane riparian as suitable cover types for fisher
HREPRO	Proportion of cells with CWHR Reproduction Rating = High

Density (EVEG)

DFOR2	Proportion of cells with cover type = Montane Hardwood-Conifer, Montane Hardwood, Ponderosa Pine, Douglas Fir, Sierran Mixed Conifer, Jeffrey Pine, White Fir, Aspen, or Eastside Pine AND CWHR Density = Dense (>60% canopy closure)
CFA80_TREE	Proportion of cells with Conifer Cover From Above (CON_CFA) or Hardwood Cover From Above (HDW_CFA) = 80–89.9% (85) OR 90–100% (95)
BADHAB	Proportion of cells with CWHR Density = S (10–24% canopy closure) or P (25–39% canopy closure) OR WHR Type = Urban or Barren

Vegetation Type Proportions (EVEG)

SMLFOR	Proportion of cells with WHR Type = Montane Hardwood-Conifer, Montane Hardwood, Ponderosa Pine, Douglas Fir, Sierran Mixed Conifer, Jeffrey Pine, White Fir, Aspen, or Eastside Pine AND WHR Size = 1 (seedling, less than 1 in. dbh) or 2 (sapling, 1–6 in. dbh)
MLFOR	Proportion of cells with WHR Type = Montane Hardwood-Conifer, Montane Hardwood, Ponderosa Pine, Douglas Fir, Sierran Mixed Conifer, Jeffrey Pine, White Fir, Aspen, or Eastside Pine AND WHR Size = 3–6 (pole to multi-layered, 6 in. dbh and higher)
LRGFOR	Proportion of cells with WHR Type = Montane Hardwood-Conifer, Montane Hardwood, Ponderosa Pine, Douglas Fir, Sierran Mixed Conifer, Jeffrey Pine, White Fir, Aspen, Eastside Pine AND WHR Size = 4, 5, or 6 (small tree to multi-layered, 11 in. dbh and up)
LRGHDWD	Proportion of cells with WHR type = MHW OR MHC AND WHRSIZE = 3, 4, 5 or 6. (pole to multi-layered, 6 in. dbh and higher)

Vegetation Type and Density (EVEG)

DLFOR	Proportion of cells with WHR type = Montane Hardwood-Conifer, Montane Hardwood, Ponderosa Pine, Douglas Fir, Sierran Mixed Conifer, Jeffrey Pine, White Fir, Aspen, or Eastside Pine AND WHR Density = D (>60% canopy closure). AND WHR Size = 4, 5, or 6 (small tree to multi-layered, 11 in. dbh and up)
STRUCT	Structure score, product of the following: CWHR habitat indicator variable (1 = Montane Hardwood-Conifer, Montane Hardwood, Ponderosa Pine, Douglas Fir, Sierran Mixed Conifer, Jeffrey Pine, White Fir, Aspen, or Eastside Pine, Red Fir, Lodgepole Pine, Subalpine Conifer, and Montane Riparian; 0 otherwise) Forest canopy closure (centroid of class interval: S (10–24%) = 17.5, P (25–39%) = 30, M (40–60%) = 50, and D (>60%) = 80)) Tree size (centroid of class interval: 1 (0–1 in. dbh) = 0.5, 2 (1–6 in. dbh) = 3.5, 3 (6–11 in. dbh) = 8.5, 4 (11–24 in. dbh) = 17.5, 5 (>24 in. dbh) = 24, and 6 (multi-layered trees) = 37)
STRUCT2	Structure score, product of the following: CWHR2 habitat indicator variable (1 = Montane Hardwood-Conifer, Montane Hardwood, Ponderosa Pine, Douglas Fir, Sierran Mixed Conifer, Jeffrey Pine, White Fir, Aspen, or Eastside Pine; 0 otherwise); Forest canopy closure (centroid of class interval: S (10–24%) = 17.5, P (25–39%) = 30, M (40–60%) = 50, and D (>60%) = 80)); Tree size (centroid of class interval: 1 (0–1 in. dbh) = 0.5, 2 (1–6 in. dbh) = 3.5, 3 (6–11 in. dbh) = 8.5, 4 (11–24 in. dbh) = 17.5, 5 (>24 in. dbh) = 24, and 6 (multi-layered trees) = 37)
CWHR_VUL	Proportion of cells with WHR type = Ponderosa Pine, Montane Hardwood-Conifer, or Sierran Mixed Conifer, AND WHR Density = D (>60% canopy closure) AND WHR Size = 3 or 4 (6–24 in. dbh)

Diversity (EVEG)

TYPE_SHDI	Shannon Diversity Index – all WHR types
TSIZE_SHDI	Shannon Diversity Index for all WHR Tree Size classes
AGGREG_SHDI	Shannon Diversity Index for aggregated WHR types/sizes/densities:

1. Low density shrubs: all Shrub habitats with density class S or P (10–39% closure, all sizes) ADS, ASC, BBR, CRC, CSC, DSW, LSG, MCH, MCP, SGB
2. High density shrubs: all shrub types with density class M or D (40–100% closure, all sizes)
3. Small hardwood forests: MHW/MRI class 1, 2, 3 (less than 1 inches to 11 in. dbh, all density classes)
4. Large hardwood forests: MHW/MRI class 4, 5 (greater than 11 in. dbh, all density classes)
5. Small, low density 'mixed conifer/pine' forests: SMC, PPN, WFR, JPN, DFR/MHC 1,2,3 (less than 1–11 in. dbh), density S and P (10–39% canopy closure)
6. Small, high density mixed conifer/pine forests as above, but density M and D (40–100% canopy closure)
7. Large, low density 'mixed conifer/pine' forests: types as above for sizes 4, 5, 6 (greater than 11 in. dbh) and density S and P (10–39% canopy closure)
8. Large, high density 'mixed conifer/pine' forests: types as above for sizes 4, 5, 6 (greater than 11 in. dbh) and density M and D (40–100% canopy closure)
9. Small high elevation forests: RFR, LPN, SCN 1, 2, 3 (less than 1 inches to 11 in. dbh)
10. Large high elevation forests: RFR, LPN, SCN 4, 5, 6 (greater than 11 in. dbh)

	11. Low elevation 'other' habitats: BOW, PGS, BOP, VRI, VOW, AGS, DRI, JST, CPC, FEW, SEW
	12. Non-vegetated habitat: BAR, URB, LAC
	13. Unique types: WTM, ASP
	14. Other 'forest' types: EPN, PJN, JUN
ALL_SHDI	Shannon Diversity Index: all Type/Size/Density
Landscape Arrangement (EVEG and FRAGSTATS)	
HREPRO_ENNMN	Mean nearest neighbor distance of HREPRO patches
CWHR2_ENNMN	Mean nearest neighbor distance of patches with CWHR2 > 0
HREPRO_AREAMN	HREPRO mean patch size
CWHR2_AREAMN	CWHR2 > 0 mean patch size
HREPRO_PARAMN	Mean perimeter–area ratio of HREPRO patches
CWHR2_PARAMN	Mean perimeter–area ratio of CWHR2 > 0 patches
Historic	
PLANT	Proportion of cells in plantations (USFS EVEG)
FIRE_OLD	Proportion of cells burned before 1990 (CA_R5_FireHistory_05_1, USFS Region 5)
FIRE_NEW	Proportion of cells burned 1990–2005 (CA_R5_FireHistory_05_1, USFS Region 5)
Tree Ages and Biomass (LANDIS-II)	
MAXAGE	Mean maximum tree age from LANDIS-II initial conditions at year 0
BIOMASS_T	Mean total tree biomass ((kg/ha)/100) from LANDIS-II initial conditions at year 0
BIOM_NORF	Mean total tree biomass ((kg/ha)/100) excluding red fir (*Abies magnifica*) from LANDIS-II initial conditions at year 0
BIOM_NORFBO	Mean total tree biomass ((kg/ha)/100) excluding red fir (*Abies magnifica*) and black oak (*Quercus kelloggii*) from LANDIS-II initial conditions at year 0
BIOM_BLKOAK	Mean black oak (*Quercus kelloggii*) biomass ((kg/ha)/100 from LANDIS-II initial conditions at year 0
Climate	
PRISM	Mean annual precipitation, 1971–2000 (United States Average Monthly or Annual Precipitation, 1971–2000, The PRISM Group at Oregon State University, 2006)
SNOWDPTH	Mean daily snow depth, January–March 2005 (National Operational Hydrologic Remote Sensing Center Snow Data Assimilation System (SNODAS): Daily Snow Depth (modeled snow layer thickness), January, February, and March 2005, National Snow and Ice Data Center, 2005)
Topography	
ADJELEV	Mean latitude-adjusted elevation. To adjust for the effect of increasing latitude, 0.625 m was added to elevation for every 1 km north from the southernmost point in the study area (National Elevation Dataset, US Geological Survey, 2006)
PCTSLOPE	Mean percent slope
RELIEF	Local relief, calculated as the standard deviation of elevation
SOUTHWEST	Mean value of transformed slope aspect (Franklin, 2003): $sw = (cos(aspect-225))$
INSOL_INDEX	Mean value of solar insolation index (Gustafson et al., 2003): $s = 2 - (sin((slope/90)180)) * (cos(22 - aspect) + 1)$.
ASPECT_225	Proportion of cells with aspect between 180 and 270 degrees
Linear features	
MJRRDDENS	Major road (primary and secondary) density (snvtran00_1, USFS Region 5, 1999; Roads of Sequoia and Kings Canyon National Parks, NPS, 2003; Roads of Yosemite National Park, NPS, 2001; USGS_ROAD100K, USGS, 1995)
ALLRDDENS	Road (all classes) density
STRMDENS	Perennial stream density (National Hydrography Dataset, US Geological Survey, 2006)

or habitat suitability models (Carroll et al., 1999; Lewis and Hayes, 2004; Zielinski et al., 2004a; California Department of Fish and Game, 2005; Zielinski et al., 2006; Davis et al., 2007), expert opinion, and hypotheses about fisher habitat relations suggested by forest managers and stakeholders. Because this work was performed in the context of a legal and socio-political conflict, the original group of potential models was very large (245) to cover a wide range of concerns and hypotheses raised by diverse stakeholder interests. This large number of original models was reduced by a series of analyses to remove models using redundant or highly correlated variables and those having little or no statistical or biological support. This winnowed our original set of models down to a reasonable set of 35 competing models with from 3 to 5 non-redundant variables each. Potential predictor variables included abiotic factors (e.g., precipitation, elevation, relief, and insolation), biotic factors (e.g., forest composition, tree size, and density variables), spatial configuration variables, and vegetation diversity indices (applying Shannon diversity to land cover data). We also tested various versions and modifications of fisher habitat value scores from the California Wildlife Habitat Relationships (CWHR) system (California Department of Fish and Game, 2005) and a revised version (CWHR2) developed by Davis et al. (2007). CWHR2 reduced the scores for upper montane, subalpine, and montane riparian forest types based on extensive field observations of fishers in California (Zielinski and Truex, Personal communications).

We also used a spatially explicit vegetation dynamics model, LANDIS-II (Scheller et al., 2007) to estimate stand age and above-ground biomass of tree and shrub species as potential predictors of fisher occupancy. We hypothesized that these continuous variables should correlate closely with forest structure characteristics that predict fisher habitat selection at fine scales, but that are difficult to comprehensively map or estimate in a GIS—such as dense, multi-storied tree canopies, abundant large trees, and abundant dead-wood structures. We therefore computed maximum age and above-ground biomass of various combinations of tree and shrub species using vegetation polygons classified by forest type, density, and tree size, and calibrated using FIA vegetation plot data that fell within each type of polygon. LANDIS-II computes these variables by simulating vegetation succession and growth processes based on life history characteristics of each species and the influence of site-specific abiotic factors (such as soils, slope, aspect, and elevation) on successional processes (see Appendix for details).

After testing a variety of moving-window sizes (from 5 to 25 km^2), we used a 5 km^2 moving window over which to average predictor variables for use in GAMs. This resolution approximates a small female fisher home range in the study area (Zielinski et al., 2004b), provides good statistical fit to the fisher detection–nondetection data, and is more discriminating of fine-scale spatial heterogeneity than larger window sizes. To reduce the potential for over-fitting or biases due to concurvity in GAM models (Ramsay et al., 2003), they were constrained to include no more than five variables and to avoid including variables likely to be correlated. For example, a model might include as a variable the proportion of the moving window in hardwood vegetation types *or* the ratio of hardwood to conifer vegetation types, but not both.

Limited tree size and density data were available in the vegetation database (EVEG) for Sequoia–Kings Canyon National Park (SEKI), which comprised 4.7% of the study area. We partially corrected for this using vegetation plot data provided by the National Park Service, but plot coverage was insufficient to confidently extrapolate tree size and density attributes across all portions of the park. For vegetation polygons in SEKI lacking density data, we used canopy density values obtained from the National Land Cover Database (NLCD) Tree Canopy Layer (2001). Polygons in SEKI missing tree size data were not altered. These inconsistencies increase uncertainty for model predictions inside SEKI for any models that used forest density or tree size variables, such as above-ground biomass.

The 35 candidate models were compared statistically to determine which model(s) best fit the MAPE2 response variable using Akaike Information Criterion (AIC) weights, percent deviance explained, residual deviance, and area under curve (AUC) of the receiver-operating characteristic (ROC) (Hastie, 1992; Altman and Bland, 1994; Fielding and Bell, 1997; Thuiller, 2003). An AUC of 0.5 indicates a model with no better discrimination than chance, an AUC of 1.0 indicates perfect discrimination, and an AUC > 0.8 indicates excellent discrimination (Hosmer and Lemeshow, 2000). We further compared the models using a temporally independent set of fisher monitoring data, the MAPE version of the fisher response variable, and fivefold cross-validation techniques. The temporally independent fisher data were obtained using similar survey protocols, at a subset of the same locations as the data used to build the models, but collected during a different time period (1998–1999 rather than 2002–2006; Zielinski et al., 2005). We applied fivefold cross-validation (Boyce et al., 2002) to estimate the degree of uncertainty around model predictions. For this, the MAPE2 dataset was randomly divided into five subsets of approximately the same size and detection/nondetection ratio. The models were estimated from 4/5 of the data and applied to the remaining 1/5. This was repeated for the other four subsets. The mean and standard deviation ROC AUC were calculated from the five prediction sets for each model and compared to ROC AUC derived from the full dataset. Finally, we examined the partial response curves for top models to better understand the relationships between each variable in the model and modeled probability of fisher occurrence, and tested the significance of the smooth terms for each variable using the chi-square test.

2.3. Population model

We used the spatially explicit and stochastic population dynamics model PATCH (Version 3.1.1.0; Schumaker, 1998) to estimate a realistic range of equilibrium population sizes (or carrying capacities) for fishers within the currently occupied habitat areas, assess what demographic or other factors most influence population size and persistence, and to identify likely population source, sink, and expansion areas. PATCH simulates occupancy of territories by individual females over time within hexagons set to average female territory size. Occupancy dynamics are functions of mean habitat value within each territory, species' dispersal characteristics, and age-specific survival and fecundity rates drawn from an age-based or stage-based population projection matrix (Leslie matrix). Stage-specific fecundity is the product of mean annual survival rate, mean percent of females producing young, mean litter size, and proportion of females in the litter (assumed to be 0.5).

We assumed that probability of fisher occurrence (P) correlates strongly with habitat value as reflected in fitness. Each 1-ha pixel on the GAM map was provided an integer score from 0 to 10 in 10% probability bins (from a score of 1 where $0 < P \leqslant 0.1$ to a score of 10 for $0.9 < P \leqslant 1.0$). The mean predicted habitat value averaged across all 1-ha pixels within a territory hexagon was used as the territory score. Territories scoring $\geqslant 7.5$ (the "ceiling" value in PATCH) were assigned relatively high fecundity and survivorship rates in a four-stage Leslie matrix (Table 2). These values were based on weighted mean survival and fecundity rates obtained from the literature (reviewed in Lewis and Hayes, 2004) modified slightly by expert opinion to provide for four age groups (stages) and to apply slightly better than average rates within high-value habitat areas. Below the ceiling value of 7.5, fecundity and survivorship were discounted linearly with territory score (x intercept = 0; exponent = 1). Lambda (intrinsic rate of population

Table 2
The four-stage Leslie matrix showing maximum fecundity and survival values, which apply for female fishers within the highest value territories (territory score >7.5). The finite rate of change (lambda) of a population characterized by this matrix would be 1.19 if all territories were high value.

Stage	0 Kits, 0–12 mo	1 Subadults, 13–24 mo	2 Subadults, 25–36 mo	3 Adults, >36 mo
Fecundity	0	0.315	0.49	1.62
Survival	0.5			
		0.7		
			0.7	0.9

growth) for the matrix of high values shown in Table 2 is 1.19, indicating that territories receiving scores >7.5 are likely to be source territories (with some variance due to landscape context and stochasticity). Territories with slightly lower scores (~6.0–7.0) have lambda ~1.0, and poor territories (score < ~5.5) are expected to be sinks (lambda < 1.0). Although there is no empirical support for a linear correlation between fisher vital rates and probability of occupancy, this assumption and the lambda estimates it produces seem defensible for purposes of estimating a range of potential equilibrium population sizes, demographic sensitivity testing, and relative comparisons between alternative forest management scenarios. Our goal was not to establish a precise quantitative estimate of population size or viability, but to assess the likely relative effects of alternative scenarios on carrying capacity under the assumption that female fishers are more likely to remain in, and therefore be detected in, high-quality territories versus low-quality territories, as reflected in vital rates.

To assess sensitivity of predicted equilibrium population sizes and trajectories to demographic parameter values, we independently decreased each stage-specific value by 5%, 10%, and 25% and observed the percent change in predicted population size. We also decreased fecundity and survivorship across all stages by these same percentages.

PATCH requires setting the territory size as an input parameter. Because population density will vary inversely with territory size, we used three fisher territory sizes that bracketed the range of territory sizes found for radio-tracked female fishers in the study area: 500 ha, 860 ha, and 1200 ha. The smallest assumed size (500 ha) was rounded down from the mean territory size of 527 ± 65.1 SE calculated by Zielinski et al. (2004b) for seven female fishers on Sequoia NF. The largest assumed size (1200 ha) was rounded up from the mean territory size of 1192 ha measured by Mazzoni (2002) for seven female fishers on Sierra NF. The intermediate size of 860 ha is the median of 527 and 1192 ha.

Site fidelity in PATCH determines the likelihood of an individual remaining on (versus abandoning) a territory from 1 year to the next. We set this to high for Stages 2 and 3 (animals >24 months old) because fishers, like the congeneric marten (*Martes americana*) (e.g., O'Doherty et al., 1997; Phillips et al., 1998), appear to maintain stable territories once established. In PATCH, individuals never give up their territories (barring mortality) when site fidelity is set to high (Schumaker, 1998). We set fidelity to medium for juveniles and yearlings (Stages 0 and 1), although young are forced to leave territories anyway as only one female can breed per hexagon. When site fidelity is set to medium, individuals will decide to move depending on territory quality and occupancy: leaving sink hexagons and remaining in source hexagons if unoccupied by another fisher.

We used the directed random walk option in PATCH to model dispersal, in which movement decisions combine some degree of randomness with a tendency to continue in the direction of the last step. Animals are attracted to higher quality habitat but have no knowledge about habitat quality beyond territories immediately adjacent to their current location. Variability in the distance and direction moved provides stochasticity. The maximum distance moved determines when the animal must settle into a territory even if it is of poor quality, but in many simulations the animal will encounter a suitable territory and settle before reaching the maximum distance. We tested maximum dispersal distances of 25, 50, and 100 km based on mean and maximum dispersal distances recorded for fishers (reviewed by Lewis and Hayes (2004)). This parameter had little or no effect on model population estimates, so for most simulations we used the intermediate value of 50 km, which was also used by Lewis and Hayes (2004).

We initialized simulations with 50, 100, or 200 adult females based on expert opinion about the likely number of females in the Sierra Nevada population. Initial population size had no significant effect on equilibrium population size regardless of other parameters (as might be expected unless populations go extinct), so for most simulations we used the intermediate starting size of 100 females. Individuals were placed on the landscape at the 100 highest value territory hexagons. All hexagons within which fishers have been detected at least once were assigned an initial value of 10 to force placement of model fishers at sites with fisher detections. After year 1, all hexagons reverted to their modeled habitat value to allow model fishers to redistribute themselves on the landscape.

For each set of territory sizes, dispersal distances, initial number of females, and demographic parameters, we ran 20 replicates for a total 40 years, but recorded results only over the final 20 years (years 21–40). Because at year 1 all animals are started at Stage-3 (adult), it can take up to ~15 years for the model population to establish an equilibrium age structure. We therefore discarded the first 20 years of results (after all modeled populations had reached a dynamic equilibrium) and recorded simulated population metrics for years 21–40 to represent the equilibrium population size, or carrying capacity, relative to current habitat conditions. Note that results over this 20-year period are not intended to explicitly represent how population size may *change* over time, because the simulations were run on a static habitat map. In reality, vegetation, habitat value, and carrying capacity are dynamic due to succession, fires, and other factors. Therefore, modeling population size over a significant time horizon required that we also simulate how forest characteristics and hence habitat quality may change over time (Spencer et al., 2008; Carroll et al., in press).

Regardless of initial population size (50, 100, or 200 females), PATCH simulations at any given territory size converge on a concordant range of equilibrium population sizes by year 40 (except for simulations where extinction occurred due to low survival rates). We therefore recorded the mean, standard deviation, median, minimum, and maximum number of females in the final year to compare results among different sets of assumptions. We also mapped and calculated the average yearly occupancy of each territory (total number of females per territory divided by 20 replicates and 20 years) and mean births minus deaths per territory (standardized by number of years and replicates tallied). The last metric, called *net value*, provides an index to identify source and sink territories.

To estimate equilibrium population size within the currently occupied region, we set habitat value to zero north of the Merced River (where fishers have not been detected in the monitoring data) to avoid having model fishers disperse and establish territories there. To assess the potential for the fisher population to expand northward under current habitat conditions, we next allowed habitat values to revert to modeled value north of the Merced River, once the model population reached equilibrium within the currently occupied region, and observed territory occupancy patterns for 200 years. Although this simulation ignored

changes in habitat due to disturbance and succession over the 200-year period, it provided a simulated baseline for evaluating the potential for northward expansion given current habitat conditions. Finally, we reduced maximum female survival rates in 5% increments from the values shown in Table 2 to investigate the sensitivity of this potential for population expansion to fisher survival rates.

3. Results

3.1. Fisher probability of occurrence

The highest ranking fisher occurrence model (LAND8; Fig. 1) accounted for 69% of the Akaike weight and achieved an AUC value of 0.941 using latitude-adjusted elevation (ADJELEV), annual precipitation (PRISM), and total above-ground biomass of trees (BIOMASS_T) as predictors. No competing model was within 2.0 AIC units of LAND8, so we chose not to average the top models. Model LAND8 also explained the greatest proportion of deviance in the fisher data, and it had the highest AUC scores of any model for the temporally independent fisher dataset, the fivefold cross-validation test, and the more inclusive MAPE interpretation of fisher occurrence data (Table 3).

All three variables contributed significantly to the predictive power of the model ($P < 0.001$ for adjusted elevation, $P = 0.003$ for annual precipitation, and $P = 0.025$ for tree biomass). Partial response curves suggest that fisher probability of occurrence increases with total above-ground forest biomass and is highest over intermediate elevations ($\sim$1300–2400 m) (Fig. 2). For those mid-elevation areas that have high forest biomass, fishers appear to favor those with less annual precipitation.

Most survey sites where fishers were not detected are in areas of very low predicted probability of occurrence, and most sites at which fisher have been detected are in areas of high predicted probability, whether using MAPE or MAPE2 as the fisher response variable (Fig. 3a and b). However, the more restrictive MAPE2 data, which excluded sample sites yielding a fisher detection in only 1 year, resulted in lower apparent errors of commission. In the MAPE data set, sites yielding a single fisher detection out of multiple survey years were often in areas of relatively low predicted probability of fisher occurrence. In contrast, sites with fisher detections in at least 2 years were rarely in areas of low predicted probability, so the MAPE2 data set seems more discriminating of fisher probability of occurrence than the MAPE data set, as hypothesized (compare Fig. 3a and b).

3.2. Population size and dynamics

The equilibrium number of adult females in model runs was largely independent of starting population size and maximum dispersal distance (Table 4), so we default to the intermediate values of 100 initial Stage-3 females and 50 km maximum dispersal distance in the following results. In contrast, equilibrium population size was strongly affected by territory size (Table 5), because population density and territory size are inversely proportional (albeit imperfectly, due to variance introduced by other factors). For reasons expanded on in Section 4, we think that using the 500-ha territory over-estimates carrying capacity, and that estimates based on the larger two territory sizes are more defensible (a range of 73–147 adult females, Table 5). We default to the intermediate territory size of 860 ha in the following results.

As should be expected for a long-lived mammal, equilibrium population size was highly sensitive to adult female survival, and relatively insensitive to changes in stage-specific fecundity or to survival in any other age group (Table 6). Reducing adult female

survival resulted in disproportionately large declines in modeled population size, with a 5% decrease in survival reducing the ending population size by more than 18%, and a 25% decrease reducing ending population size by more than 72%. In contrast, reducing any other stage-specific survival or fecundity rate had a disproportionately small effect on ending population size. When survival was simultaneously reduced by 25% across all age classes, the simulated populations crashed: 8 of 20 runs resulted in extinction before the end of the 20-year period, with no more than two adult females remaining in the other 12 runs. Simultaneously reducing fecundity across all ages had a much smaller effect, with only a 9.2% decline in average population estimate and no extinctions.

Model territories that were most reliably occupied over time clustered in relatively narrow bands of mid-elevation forests in association with the largest contiguous blocks of high-value habitat (Fig. 4). These same areas also tend to be predicted source territories (Fig. 5). Less reliably occupied territories, including many predicted sink territories, tended to be adjacent to source territories, or were scattered farther away in areas of moderate predicted habitat value. The strongest predicted sink territories (red in Fig. 5) were generally moderate-value territories immediately adjacent to high-value source territories, because such territories have a high probability of being settled by dispersing fishers, but deaths exceed births within them. Note that sparsely used territories in SEKI reflect missing environmental data, which probably resulted in under-estimation of forest biomass and hence modeled occupancy there.

When we allowed habitat value north of the Merced River to revert from zero to modeled habitat value, the model population gradually expanded northward into mostly moderate-value habitat over about the next 100 years, eventually contributing to a larger equilibrium population of 173 ± 17.2 SD adult females, compared to 135 ± 8.1 SD using the same parameter values in the spatially constrained runs. The northern front of this modeled colonization event stalled about 80 km north of the Merced River (the inserts in Figs. 4 and 5) in a region where modeled habitat value generally drops below 0.5.

The simulated expansion was highly sensitive to maximum survival rates: Predicted territory occupancy north of the Merced River dropped with each 5% decrease in survivorship, with no expansion north of the Tuolumne River occurring when the maximum survival rates assumed in Table 2 were reduced by 15%, and no expansion north of the Merced River when survival rates were reduced by 20% (Fig. 6).

4. Discussion and conclusions

Our combined models, linking spatially explicit occupancy and population analyses, provide a useful tool for assessing conservation strategies and restoring imperiled populations. The fisher probability of occurrence model provides a regional context for finer-resolution assessments of fisher habitat relations (e.g., Mazzoni, 2002; Zielinski et al., 2004a,b, 2006; Jordan, 2007). Coupling it with a spatially explicit population model provides a better understanding of how both the value and spatial configuration of habitat may affect the fisher population and where habitat management actions may be most beneficial.

4.1. Habitat characteristics and distribution

Our approach to modeling fisher probability of occurrence and habitat value complements and builds on the work of Davis et al. (2007) who modeled fisher habitat throughout California and in three subregions, including the southern Sierra Nevada. Our approach differed in that it: (1) used additional fisher monitoring data
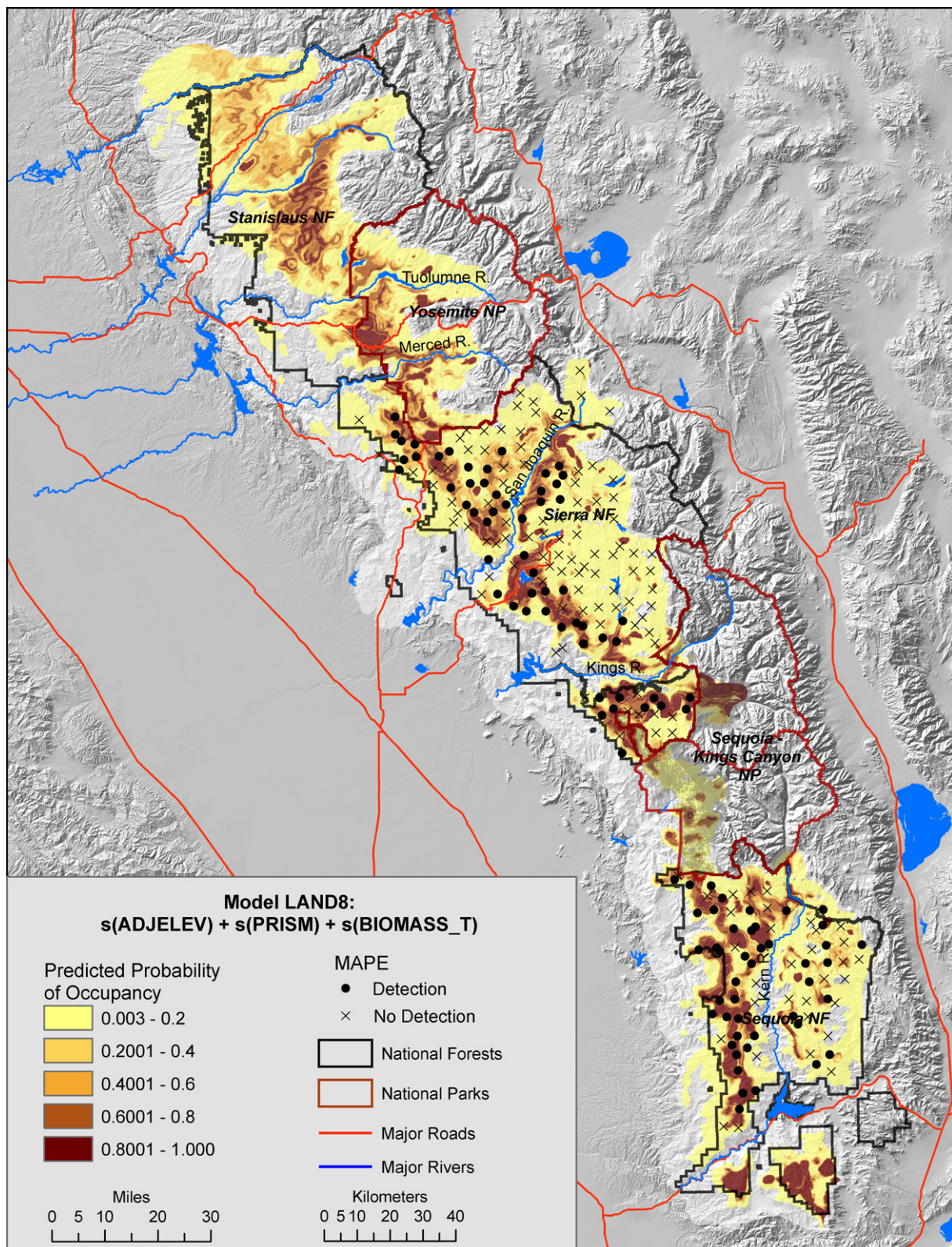
Fig. 1. Predicted fisher probability of occupancy from the GAM model LAND8 using adjusted elevation, annual precipitation, and total tree biomass within a 5 km² moving window and compared with fisher detection–nondetection monitoring data. Data gaps for tree size probably result in under-prediction of habitat value in portions of Sequoia–Kings Canyon NP.

that allowed a more rigorous interpretation of fisher presence versus absence (i.e., MAPE2); (2) was at finer resolution (5 km² versus 10 km²); (3) produced models that better fit the fisher occurrence data (AUC = 0.94 versus 0.61–0.73); and (4) included model testing using a temporally independent fisher data set. Our best fisher probability of occurrence model used the same two abiotic variables as

Table 3
Statistical comparison of the top 10 fisher habitat GAM models, ranked in descending order by AIC weights. Metrics also include delta AIC, % deviance explained; area under curve (AUC) for the receiver-operating characteristic using the MAPE2 (conservative) and MAPE (liberal) interpretations of the fisher detection–nondetection data; AUC for the temporally independent fisher survey data test data set (Zielinski et al., 2005); and the mean and standard deviation of the fivefold cross-validation test using MAPE2.

Model	Variables	AIC$_c$ weights	Delta AIC	Proportion deviance explained	AUC MAPE2	AUC MAPE	AUC TEST SET	Mean fivefold cross-validated AUC	SD fivefold cross-validated AUC
LAND8	ADJELEV, PRISM, BIOMASS_T	0.68974	0.0000	0.53260	0.94097	0.83145	0.63828	0.90499	0.07079
LAND7	ADJELEV, INSOL_INDEX, BIOMASS	0.15767	2.9516	0.51768	0.93302	0.82264	0.61370	0.90332	0.05452
LAND13	ADJELEV, INSOL_INDEX, MAXAGE, BIOMASS_T	0.05790	4.9554	0.51829	0.93372	0.82092	0.61370	0.89888	0.05642
LAND1	ADJELEV, INSOL_INDEX, MAXAGE	0.04921	5.2806	0.50591	0.93001	0.82755	0.59438	0.87871	0.04170
LAND14	ADJELEV, INSOL_INDEX, MAXAGE, BIOM_NORF	0.03415	6.0110	0.51296	0.93478	0.82685	0.59350	0.87069	0.04578
LAND3	ADJELEV, PRISM, MAXAGE	0.00732	9.0912	0.48666	0.92294	0.82732	0.62511	0.88197	0.06829
LAND11	ADJELEV, INSOL_INDEX, BIOM_NORFBO, BIOM_BLKOAK	0.00205	11.6333	0.48454	0.92153	0.81375	0.59087	0.89119	0.05815
LAND10	ADJELEV, INSOL_INDEX, BIOM_NORF	0.00091	13.2583	0.46560	0.92082	0.82015	0.63652	0.87956	0.03619
LAND15	ADJELEV, INSOL_INDEX, BIOM_NORFBO, BIOM_BLKOAK, MAXAGE	0.00070	13.7838	0.48454	0.92153	0.81375	0.59087	0.89119	0.05815
LAND12	ADJELEV, INSOL_INDEX, BIOM_BLKOAK	0.00011	17.4021	0.44466	0.90597	0.80393	0.61896	0.88232	0.06142

Davis et al. (2007) for the southern Sierra Nevada (latitude-adjusted elevation and annual precipitation) but different biotic variables. These results suggest that the abiotic variables elevation and annual precipitation interact to establish the physical potential of a site to support fishers, even though they cannot account for disturbance history, which affects vegetation characteristics important to fishers (e.g., forest biomass and canopy closure). In addition to establishing the potential to support forest vegetation favorable to fishers, elevation and precipitation interact to establish the physical conditions directly experienced by fishers. Because much of the precipitation in the Sierra Nevada falls as winter snow, these results support the hypothesis that fishers favor areas that accumulate less snow, because fishers are not highly adapted for traveling and foraging in deep snows (Krohn et al., 2004).

Total above-ground biomass of trees was the strongest biotic predictor of fisher habitat value in our models, rather than more specific forest composition or structure variables, such as tree species, size, and density variables used in previous models (Carroll et al., 1999; Zielinski et al., 2006; Davis et al., 2007). Total forest biomass will increase with both site productivity and stand age, and it should correlate closely with forest structure variables found by numerous field studies to predict fisher habitat selection at fine scales: large trees, dense, multi-storied canopies, and abundant dead-wood structures (Carroll et al., 1999; Mazzoni, 2002; Zielinski et al., 2004a,b, 2006). Our results suggest that, at the landscape scale, total tree biomass tends to be a good predictor of fisher habitat quality, probably because it represents these various constituent elements (which are difficult to comprehensively map or estimate in GIS) within one continuous and robust variable that can be comprehensively mapped (see Appendix A). Thus, we predict that, in general, vegetation management, fires, and other disturbances that decrease forest biomass or fragment areas of high biomass will have adverse effects on fishers, and that factors promoting accumulation of forest biomass may benefit fishers. However, it is also important to consider how forest biomass is distributed within forest stands—for example, whether the majority of biomass is accounted for by few large trees versus many smaller trees—to ensure that the finer-scale structural elements needed by fishers are also present. Vegetation management that promotes accumulation of forest biomass but that removes important constituent elements, such as dead-wood structures, deformed trees, or trees with cavities may be detrimental in ways our landscape-scale correlation model cannot account for.

The fisher population in the southern Sierra Nevada is concentrated within a relatively narrow band (roughly 5–15 km wide over most of its length) of forest between about 1400 and 2300 m elevation, mostly on the western slope of the range. This narrow distribution pattern puts the population at risk of fragmentation by large, severe fires or other disturbances. Fuels management projects should be strategically located to minimize risks of severe fires that could further reduce and fragment the habitat (Spencer et al., 2008).

Habitat generally declines in suitability and becomes more fragmented moving north from Yosemite NP. This is consistent with observations by others suggesting that the >400 km gap in fisher occupancy through the central and northern Sierra Nevada is at least partly due to habitat alterations that reduced habitat quality and contiguity there (Zielinski et al., 2005; Davis et al., 2007). However, according to our models and those of Davis et al. (2007), there is some suitable but unoccupied habitat north of the Merced River within and adjacent to Yosemite NP. Focused surveys have failed to confirm fishers in this area, although there are occasional incidental sightings of individuals or tracks (Chow, 2009). Jordan (2007) hypothesized that dramatic river canyons like the Merced (aka, Yosemite Valley) may be strong filters to fisher dispersal due to extremely steep terrain, large areas of sparsely forested vegetation, large rivers, and heavily traveled roads. The occasional sightings north of the Merced (Chow, 2009) suggest that these features are not absolute barriers, although they may limit dispersal or increase mortality during dispersal. Davis et al. (2007) speculated that low vital rates within occupied habitats may be limiting the supply of emigrating individuals for northward expansion; and Chow (2009) speculated that additive mortality in and near Yosemite NP, especially roadkill, may be hindering population recovery following the adverse effects of trapping and logging in the early 20th Century. Our models lend support to this hypothesis by demonstrating that even modest increases in mortality rates (~10–20%) could prevent population expansion, even in the absence of dispersal barriers. Ongoing field studies for the Sierra Nevada Adaptive Management Plan (SNAMP) further support this hypothesis, as researchers are finding evidence of elevated fisher mortality in and just south of Yosemite NP due to human influences (including roadkill and diseases carried by domestic cats and dogs) – with an average female survivorship of only 0.74 estimated from January 2008 to August 2010 (R. Sweitzer and R. Barrett, Unpublished data). This rate is
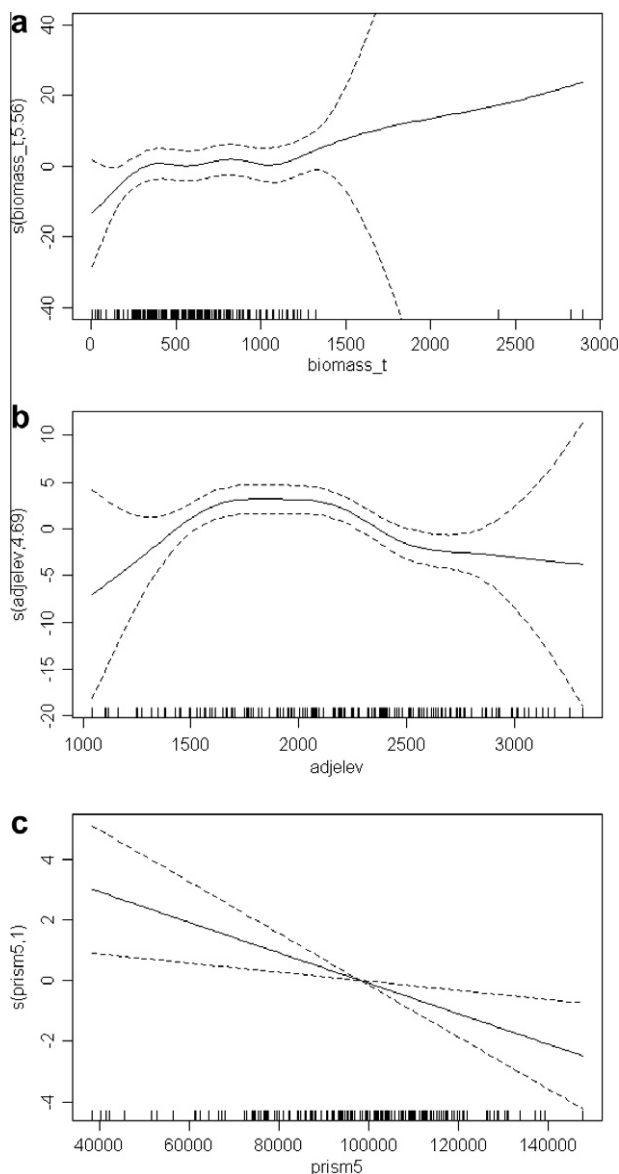
Fig. 2. Partial response curves for the GAM model LAND8. The *x*-axis is the value of the model independent variable, and the *y*-axis is the additive contribution of the variable to the nonparametric GAM smoothing function. Dashed lines are two standard errors about the estimated function. Variables: (a) total above-ground biomass of trees in kg/ha/100 (BIOMASS_T); (b) latitude-adjusted elevation in meters (ADJELEV); (c) annual precipitation in mm ∗ 100 (PRISM).

Fig. 3. Accuracy of the probability of fisher occurrence model LAND8 in predicting fisher presence and absence using: (a) the more inclusive MAPE interpretation of the fisher data and (b) the more restrictive MAPE2 interpretation of the fisher data. MAPE2 omits sites surveyed only once or with only one fisher detection despite multiple surveys; MAPE includes all sites. Shaded bars represent survey sites lacking detections; open bars are those with detections. Note that the MAPE interpretation results in more fisher detections in areas of low predicted fisher probability of occurrence (i.e., apparent errors of commission).

about 18% lower than the maximum adult female survival rate we used (0.90) and consistent with our finding that a 10–20% reduction in survivorship would interfere with population expansion. We conclude that elevated mortality, perhaps in concert with dispersal filters, is likely interfering with natural reestablishment of a breeding population north of Yosemite Valley, and that land managers should investigate ways of reducing such additive mortality factors. North and west of Yosemite NP, management on Stanislaus NF should strive to sustain and recover late-seral forest conditions (i.e., high forest biomass and structural diversity) and prevent large-scale disturbances (e.g., severe crown fires) to further facilitate northward population expansion – which our models suggest represents the greatest potential to increase the population's size and viability.

It is uncertain whether natural expansion, perhaps aided by vegetation management and succession, can re-establish a contin-
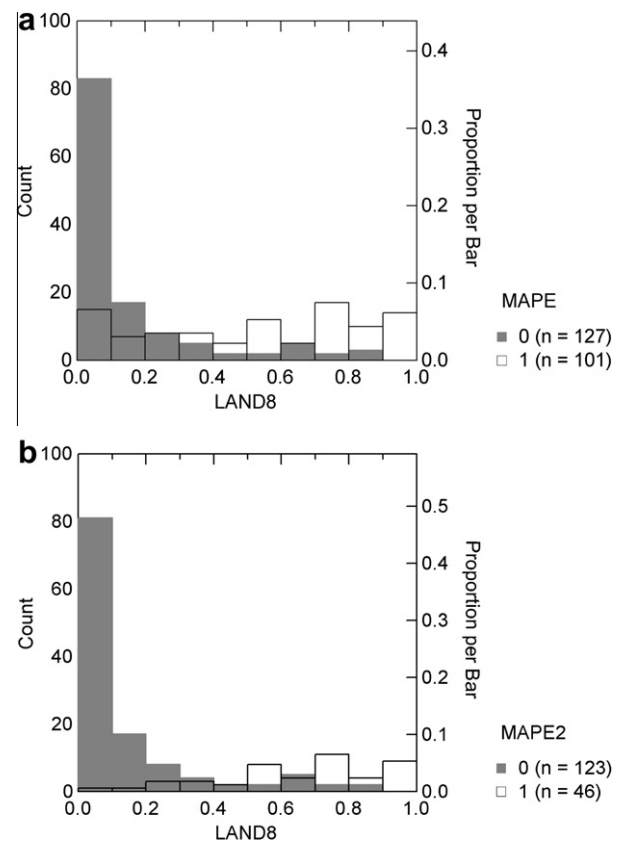
Table 4
Effects of initial population size and maximum dispersal distance on modeled number of adult female fishers at equilibrium (model year 40) with 20 replicates each. Starting population size was varied as 50, 100, or 200 adult females using 860-ha territory size and 50 km maximum dispersal distance. Maximum dispersal distance was varied as 25-, 50, or 100 km using 860-ha territory size and 100 initial adult females.

	Mean	SD
Initial population size		
50	131.2	10.25
100	134.8	8.07
200	141.0	8.82
Maximum dispersal (km)		
25	132.2	8.96
50	134.8	8.07
100	137.4	10.25

Table 5
Effects of territory size on modeled number of adult females at equilibrium (model year 40). All simulations started with 100 Stage-3 females; 50 km maximum dispersal distance, 20 replicates.

Territory size (ha)	Median	Mean	Min	Max	SD
500	255.5	255.2	241	273	7.64
860	135.5	134.8	121	147	8.07
1200	90.0	89.5	73	106	8.87

Table 6

Sensitivity of the equilibrium population estimate (number of adult females at year 40) to demographic parameters. Each fecundity and survival rate was decreased by 5%, 10%, and 25% while holding all others at default values (see Table 2). Percent change is relative to mean population estimate for the default model. Territory size = 860 ha; dispersal distance = 50 km; initial population = 100 adult females; 20 replicates for each set of values.

Parameter varied	25% Decrease			10% Decrease			5% Decrease		
	Mean	SD	% Change	Mean	SD	% Change	Mean	SD	% Change
None – default	134.8	8.07							
S1 fecundity	135.05	10.07	0.19	136.15	5.64	1.00	137.40	7.75	1.93
S2 fecundity	134.7	8.69	−0.07	136.30	9.23	1.11	138.15	9.71	2.49
S3 fecundity	123.85	9.16	−8.12	131.15	10.28	−2.71	134.05	10.47	−0.56
S0 survival	115.35	7.04	−14.43	129.80	7.50	−3.71	130.95	9.89	−2.86
S1 survival	112.15	8.43	−16.80	124.65	9.76	−7.53	131.35	7.82	−2.56
S2 survival	109.65	9.11	−18.66	129.15	10.07	−4.19	129.90	9.83	−3.64
S3 survival	36.9	7.58	−72.63	84.90	10.21	−37.02	110.15	10.86	−18.29
All stages fecundity	122.45	5.57	−9.16	133.30	9.33	−1.11	135.35	7.75	0.41
All stages survival	0.6	0.68	−99.55	54.90	8.36	−59.27	94.20	7.24	−30.12

uous, connected fisher population through the >400 km gap separating the southern population from a larger population in the north Cascade and Klamath Mountains in northern California. Moreover, the increasingly severe fire regime in the Sierra Nevada, coupled with effects of climate change (Westerling et al., 2006; Miller et al., 2008) could interfere with natural forest and fisher recovery. Exploring implications of these issues for the fisher requires application of a dynamic landscape change model that simulates disturbance and succession effects on fisher habitat (Spencer et al., 2008; Carroll et al., in press). Regardless of uncertainty about future conditions, forest management actions should attempt to maximize contiguity and integrity of high biomass, mixed-coniferous forest stands in this region.

Predicted sink habitat areas adjacent to higher quality areas should not be viewed as management "sacrifice zones" that are unimportant to or even detrimental to fisher persistence. Individual fishers may temporarily occupy marginal habitat until a better territory becomes available. Because sink territories are more likely to support subadult fishers with low fecundity, and source territories are more likely to support adults with high fecundity, maintaining and increasing habitat value in current sink areas can help support individuals until they can move into and reproduce within a higher quality territory. In addition, some marginal habitat areas are likely to increase in value via vegetation succession following past disturbances, further increasing the size and productivity of contiguous high-quality habitat blocks.

4.2. Population size and dynamics

Assumptions of the spatially explicit population model create uncertainties for absolute predictions about population size or dynamics. Most notably, our assumption that fisher vital rates scale with probability of occupancy (or habitat value) could be questioned as lacking empirical support. However, the lambda estimates and spatial patterns produced by the model seem biologically defensible and fit data emerging from fisher field studies in the region (Sweitzer and Barrett, Unpublished data from the SNAMP, and Thompson and Purcell, Unpublished data from the Kings River Fisher Project on Sierra NF). The biological reasoning behind the assumption is that female fishers are most likely to remain in, and therefore be detected in, territories where they are most likely to survive and reproduce. The precise form of the relation between habitat and vital rates is not critical, given that the intent is not so much to produce precise population estimates as to produce a reasonable range of carrying capacity estimates to facilitate *relative* comparisons between alternative scenarios and assess the population's sensitivity to various assumptions. Moreover, the patterns of territory occu-

pancy and demographic rates being measured by intensive field studies in our study area (using telemetry, GPS collars, and survey arrays) seem quite consistent with the patterns predicted by our models (Sweitzer and Barrett, Personal communications and Unpublished data presented at the SNAMP Fisher Integration Meeting, July 22, 2010; http://snamp.cnr.berkeley.edu/static/documents/2010/08/13/Sweitzer_Barrett_FisherIT_Year3Update_Fresno_20100722.pdf). For example, the SNAMP study measured average female survival and fecundity rates of 0.74 and 1.60 during January 2008 to August 2010 (across a range of habitat values). These compare favorably with our *maximum* estimates of 0.90 and 1.62 in high-quality habitat (territory score >7.5) – except that measured female survivorship is about 18% lower than our maximum rate, and is consistent with the hypothesis that elevated mortality due to human influences may be interfering with northward expansion of the fisher population.

As expected for a long-lived mammal, we found that equilibrium population size was highly sensitive to adult female survival, and relatively insensitive to changes in stage-specific fecundity or to survival in any other age group. The elasticity relationships we observed among vital rates and population size are similar to those reported for other medium and large carnivorous mammals that mature relatively late in life (Heppell et al., 2000).

We believe that population (or carrying capacity) estimates based on the smallest territory size we tested (500 ha) are inflated and that estimates based on larger territory sizes (860–1200 ha) are more defensible. The 500-ha territory estimate was rounded down from the mean of seven female territories measured in very high-quality habitat on the Sequoia NF (527 ha; Zielinski et al., 2004b) which is the smallest average fisher territory size recorded in North America. A second radio-tracking study in our study area yielded female territory sizes closer to those measured elsewhere (mean = 1192 ha for seven females; Mazzoni, 2002). More recently, two intensive telemetry studies in the northern and central portions of our study area have yielded larger average female home range sizes than the territory sizes we assumed: The SNAMP study measured average home range size for 19 adult females during 2008–2010 of 2620 ± SE 210 ha using 90% fixed kernels (Sweitzer and Barrett, Unpublished data); and the Kings River Fisher Project measured average annual female home range size of 1917 ± 199.5 SE ha using 95% fixed kernels (N = 37) (Thompson et al., 2010). Given that the territory hexagons in PATCH should approximate the size of female territories averaged across the range of occupied habitat qualities in the study area, and given the tremendous heterogeneity of habitat in the region, we surmise that the territories recorded by Zielinski et al. (2004b) are too small to be representative. We therefore relied on model runs using territories of 860–1200 ha to estimate fisher carrying
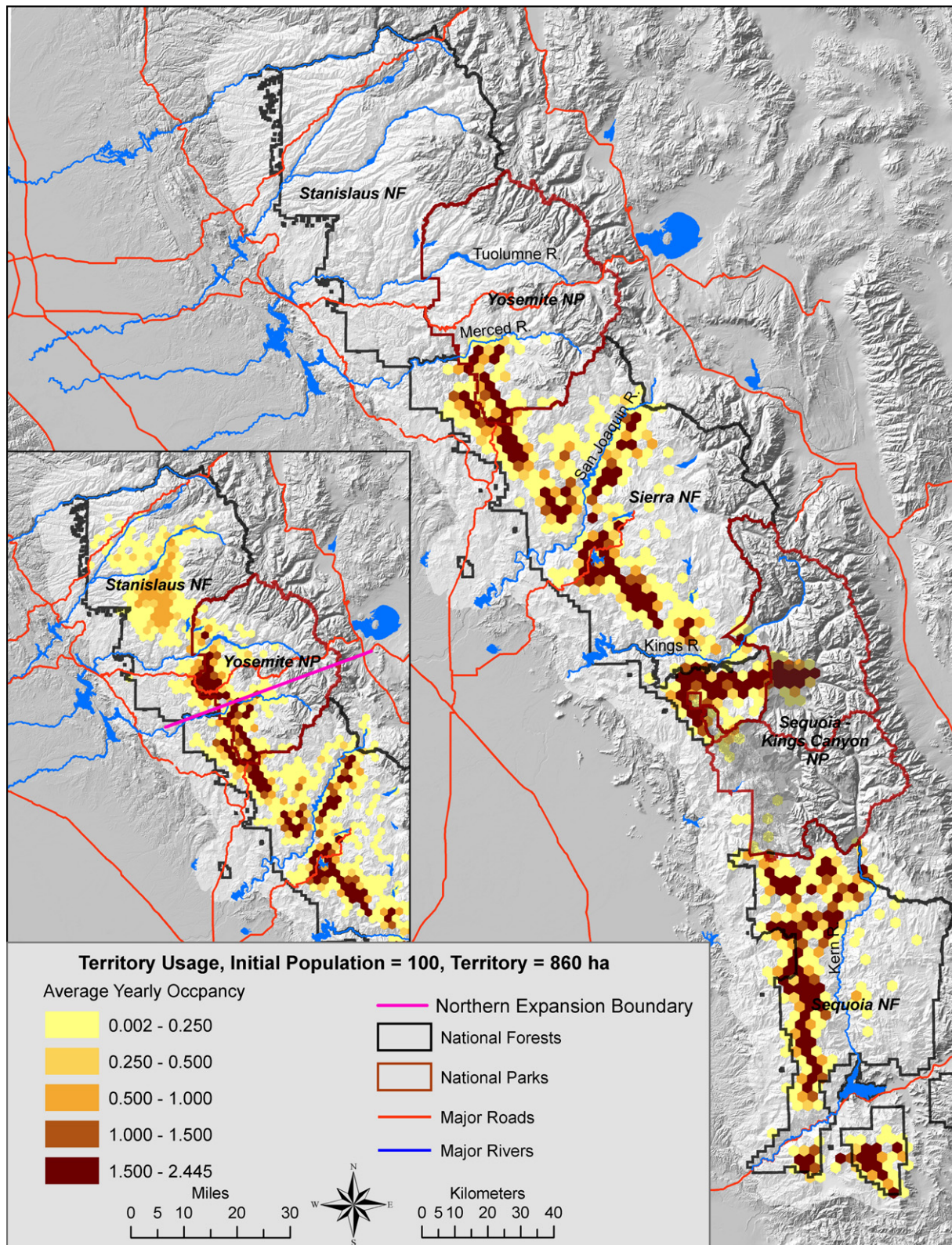
Fig. 4. Average annual territory occupancy predicted by PATCH using intermediate parameter values (860-ha territory size, 100 initial females, 50 km dispersal distance) averaged over 20 replicates. Territory usage includes juvenile females sharing a mother's territory, so highly productive territories can have average yearly occupancies >1.0. The inset shows expansion of the model population north of the Merced River (magenta line) over 200 years for comparison with the other map, where fishers were constrained to the currently occupied area south of the Merced River. Data gaps probably result in under-representation of habitat value and hence territory value in Sequoia–Kings Canyon NP.

capacity in the study area, and this might nevertheless over-estimate carrying capacity if average territories are actually larger than 1200 ha.

Assuming the currently occupied habitat area supports 73–147 adult females (from the range of equilibrium population estimates for 860- and 1200-ha territories; Table 5), and assuming a 1:1 adult
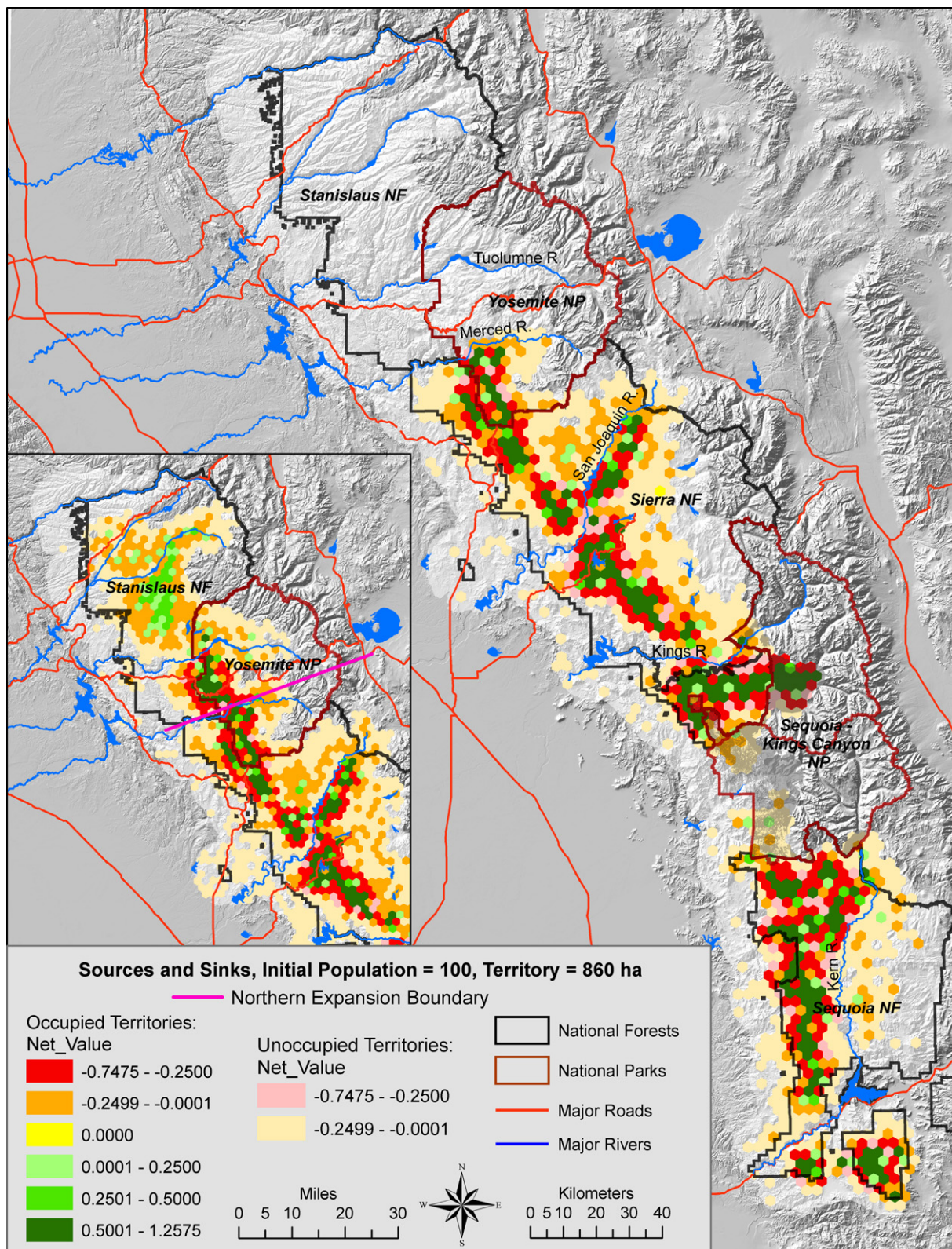
Fig. 5. Net value of territories (annualized births–deaths) observed using intermediate parameter values (860-ha territory size, 100 initial females, 50 km maximum dispersal) averaged over 20 replicates. Source territories are in greens and sink territories in reds. The inset shows expansion of the model population north of the Merced River (magenta line) over 200 years for comparison with the other map, where fishers were constrained to the currently occupied area south of the Merced River. Data gaps probably result in under-representation of occupancy and territory value in Sequoia–Kings Canyon National Park.

sex ratio, the estimate of total adult population size would be 146–294 fishers. However, this probably over-estimates the number of males, because field studies in the area have found female-biased

sex ratios and higher male mortality rates (Sweitzer and Barrett, Unpublished data; Jordan, 2007; Thompson et al., 2010) as well as significantly larger male than female home ranges (Zielinski
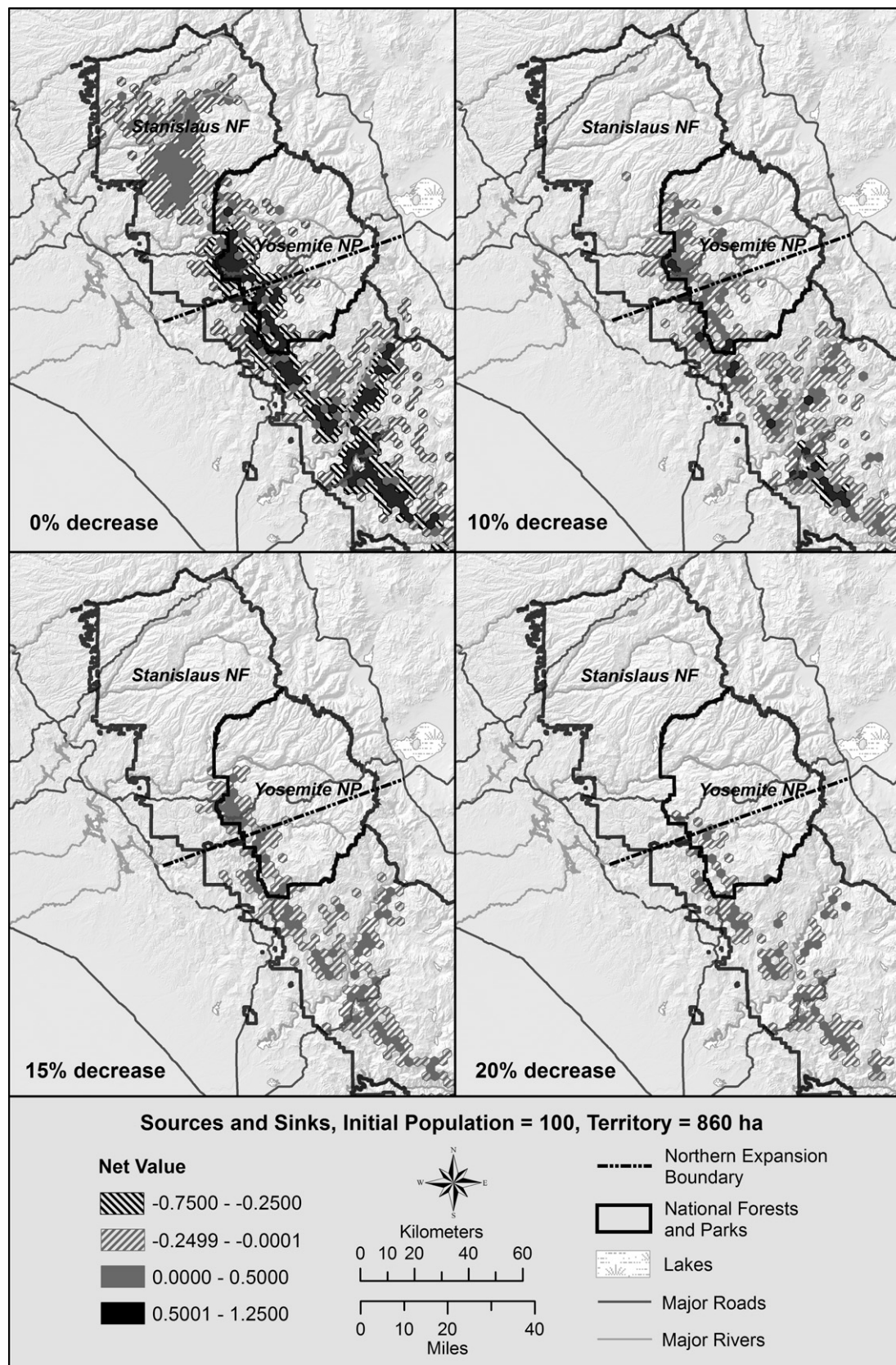
Fig. 6. Effects of increasing mortality rates on potential for population expansion. Explanations the same as Fig. 5, except that maximum survival rates were reduced by 0%, 10%, 15%, and 20% in the four panels which show the northern portion of the study area.

et al., 2004b; Sweitzer and Barrett, Unpublished data; Thompson et al., 2010). We therefore conclude that the current population probably includes less than ~300 adult fishers. These estimates

accord reasonably well with an estimate extrapolated from fisher density calculated by Jordan (2007) based on 3 years of mark-resight data recorded at camera traps on the Sierra NF. We

extrapolated Jordan's density estimates (10–13 total fishers, of which 2–3 are adult females, per 100 km^2) over our modeled fisher occupancy area (using the 0.5 probability cut point to define occupied habitat). This provided an estimate of 55–83 adult females, or 276–359 total fishers, which includes an unknown number of subadults and perhaps juveniles not counted in our carrying capacity estimates.

Regardless of the precise number of fishers in the population, wildlife populations this small (i.e., of at most a few hundred individuals) are at risk of extirpation from a variety of causes, including stochastic events (Shaffer, 1981; Traill et al., 2009). Moreover, the *effective population size* (Wright, 1931) of this isolated population could be quite small, and indeed Wisely et al. (2004) found the southern Sierra Nevada population to be the most genetically depauperate in the fisher's Pacific coast distribution. These realities heighten the urgency of efforts to increase the fisher population and to protect and restore fisher habitat in the Sierra Nevada.

4.3. Conclusions

Spatially explicit occupancy and population models are useful tools for generating hypotheses to be tested in adaptive management and monitoring programs and guiding conservation actions (Carroll, 2006; Carroll et al., in press). Although the models we present here are providing useful hypotheses for field research and adaptive management in the study area (Sweitzer, Personal communication), their utility for forecasting alternative futures for the population is limited by the static nature of the fisher probability of occurrence map. To make useful predictions about the future of the population under alternative conservation strategies—particularly in light of changing climate, fire regimes, and forest management practices—requires that the predictive habitat map be dynamic, changing realistically in response to alternative assumptions about how fires, climate, management, and other factors may affect habitat over time. Our models of occupancy and demography have therefore been expanded to also accommodate simulated changes in habitat conditions, thus providing a means of comparing the likely relative effects of alternative future scenarios on the southern Sierra Nevada fisher population (Spencer et al., 2008; Carroll et al., in press). For example, the coupled models can be used to inform strategies for siting, designing, and phasing fuels treatments to minimize biomass removal (by both fuels treatments and fires) and to maximize the potential size of the fisher population in the face of increasingly severe fire conditions.

Acknowledgements

Appendix A

We used the vegetation dynamics model LANDIS-II (Scheller et al., 2007) to derive forest biomass and stand age estimates at 1-ha resolution using vegetation map data, Forest Inventory and Analysis (FIA) plot data, and topographic, climate and other data. To map contemporary vegetation conditions in a manner suitable for LANDIS-II (which tracks biomass of species-age cohorts over time across the landscape) we began with the California EVEG map (which divides the landscape into polygons of relatively homogeneous overstory vegetation based on predominant species, tree size, and canopy density). We updated the EVEG map to account for recent disturbances (particularly clearcuts) using satellite imagery and harvest data. We then combined the forest composition, size, and density attributes of the EVEG map (from the California Wildlife Habitat Relationship (CWHR) database) with FIA vegetation plot data to create a new vegetation map having empirically derived estimates of forest composition, age, and biomass, as follows.

We first aggregated over 2 million, 1-ha forested cells in our study area into seven land types that represent relatively homogeneous climatic and soil conditions that influence how tree and shrub species establish and grow (and how establishment, growth, and death are simulated in LANDIS-II). Six land types were derived using supervised and unsupervised clustering analyses applied to elevation, slope, insolation index, minimum January temperature, maximum July temperature, and precipitation. A seventh land type was added using satellite classification of permanent shrub fields.

FIA plot data (608 FIA plot locations total) were used to estimate contemporary community composition and age in mapped EVEG polygons using 23 tree and two shrub species that are common in the study area. Each FIA-derived list of species and age cohorts was assigned a CWHR type based on the dominant overstory tree(s), and each FIA plot was assigned a CWHR size class (in inches: <1, 1–6, 6–11, 11–24, >24), based on the 75th percentile diameter for all trees on the plot. Age of tree cohorts was estimated using a regression between stem diameter (natural log transformed) and FIA stand age estimates drawn from all 608 plots. Trees and shrubs were then binned into 5-year species-age cohorts.

The relationships established between CWHR designations and FIA plot data were then used to extrapolate stand conditions derived from FIA data across EVEG polygons. The transformed vegetation data from the 608 FIA plots were randomly assigned to each of the 600,000 + EVEG polygons based on similarity of tree sizes and community type, thus creating contemporary community conditions for the entire landscape.

Based on this map, the LANDIS-II Biomass Succession extension (version 2.0) was used to calculate total above-ground biomass (kg/ha) of forest stands across the landscape. The Biomass Succession extension uses the probability of establishment (P_{EST}) and aboveground net primary productivity (ANPP) for each species and land type to simulate above-ground biomass (AGB) as a function of age. These parameters were estimated through consultation with US Forest Service silviculturists and calibrated using Forest Vegetation Simulator (FVS) results for 24 sample sites across the study area (Spencer et al., 2008). The Biomass Succession extension "spins up" contemporary AGB for each species-age cohort from the FIA-generated species-age list by growing the cohort for a period corresponding to its age. At the end of the spin-up phase, each species-age cohort has an estimated AGB, from which we calculated the total AGB for all species combined or

for subsets of species hypothesized to be important to fisher habitat value (Table 1).

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