<cn>Chapter 18

<ct>Use of Habitat and Viability Models in *Martes* Conservation and Restoration

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<A>Abstract

<txf>Conservation and management of *Martes* populations are increasingly informed by quantitative models that predict habitat suitability and population viability. Recent modeling efforts to support fisher (*Martes pennanti*) reintroduction planning in the state of Washington and conservation of an isolated fisher population in the southern Sierra Nevada (California, USA) have integrated results from empirical static habitat models, such as resource-selection functions, with those from dynamic population-viability and vegetation models. Additional methods have been developed to identify habitat linkages with potential importance for maintaining interpopulation dispersal. While such modeling frameworks can be useful in integrating data on species distribution, demography, and vegetation response to disturbance, the associated increased data requirements may also increase uncertainty regarding model projections to different places or times. The costs associated with reintroductions generally justify the use of such models to inform the planning process before substantial resources are committed. Given the challenges posed by increasing human demands on forest ecosystems, well-constructed quantitative models can be key tools for enhancing the success of wildlife conservation efforts, as long as model uncertainty is considered explicitly, and model results are used for informing decisions rather than predicting outcomes.

<A>Introduction

<txt>Conservation and management of *Martes* populations are increasingly informed by quantitative models that predict habitat suitability and population viability. Statistical models of habitat relations can help increase understanding of the factors limiting a species' distribution, facilitate protection and enhancement of habitat, predict distribution in unsurveyed areas, and evaluate suitability of currently unoccupied areas for reintroduction. More complex population-viability models that integrate data on habitat and demography are also increasingly employed to evaluate the effects of alternative management options on population persistence.

Like many carnivores, North American *Martes* species (American marten [*M. americana*], and fisher [*M. pennanti*]) have undergone range contractions since European settlement (Krohn, this volume). Although both species retain large populations over much of their historical ranges, several regional subpopulations are of conservation concern (Krohn, this volume). Whereas overexploitation was a primary factor contributing to range contractions historically, current threats stem primarily from widespread habitat alteration due to intensive forestry and other factors (I.D. Thompson et al., this volume). Thus, conservation and management of existing populations may involve evaluation of both local- and regional-scale habitat suitability (Shirk et al., this volume). Planning at broader spatial scales may involve development of quantitative habitat suitability models from geographically extensive data, such as satellite imagery (Carroll et al. 1999; Spencer et al. 2011; Marcot and Raphael, this volume).

To reverse range contractions stemming from historical overexploitation, American martens and fishers have been translocated to many areas (Drew et al. 2003; Powell et al., this volume). Although early reintroductions often were based on qualitative assessments of the availability of suitable habitat, more recent efforts have typically involved quantitative modeling of habitat suitability (Lewis and Hayes 2004; Callas and Figura 2008). Reintroductions, especially in eastern North America, have frequently been successful in establishing populations (Aubry and Lewis 2003; Powell et al., this volume). However, at least 2 aspects of the demography and habitat associations of North American *Martes* species may create challenges for both reintroduction and conservation of small populations (Powell et al., this volume). *Martes* species generally have relatively large territory sizes for their body mass (Powell and Zielinski 1994). Additionally, dispersal ability for the majority of species may be limited by their association with forest habitats (Powell and Zielinski 1994).

In this chapter, we review the types of habitat and viability models that have been used to guide conservation efforts for North American *Martes* species (Table 18.1). The types of habitat and viability models reviewed here fall into 4 distinct categories based on their output predictions: distribution, dispersal, persistence, and optimal reserves (Table 18.1). Each type of model can be characterized by its data structure (i.e., types of input and output data), treatment of uncertainty, and context in the planning process. We present 2 case studies for the fisher in western North America that provide guidelines for choosing and applying appropriate modeling tools, and may be useful for *Martes* conservation efforts in other regions. Such planning tools are particularly relevant for the fisher, which in 2004 was classified as “warranted but precluded” from listing as a threatened species under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service 2004). This finding has motivated land-management agencies to evaluate important habitat areas for the species in the Pacific coastal states and provinces (Lofroth et al. 2011).

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<A>Models of Distribution and Resource Selection

<txt>The first habitat models used to inform *Martes* reintroduction efforts were conceptual models such as the Habitat Suitability Index (HSI), that allowed expert opinion on the value of various habitat types to be expressed formally as a quantitative index (Allen 1983). The maximum value in Allen’s (1983) fisher HSI model occurs when canopy closure is >75%, mean diameter at breast height (dbh) of overstory trees is >40 cm, 3 or more tree species are present in the canopy, and 10–50% of the overstory is deciduous. Thomasma et al. (1991) used Allen’s (1983) model to inform a fisher reintroduction effort in the Upper Peninsula of Michigan. A comparison of the HSI model predictions with snow-tracking data revealed that, although the composite HSI score was a significant predictor of fisher habitat use, only 2 of the 4 component variables (mean dbh of overstory trees and percentage of overstory deciduous trees) were significant in the multivariate model. In addition, the shape of the response function was not monotonically increasing, but multimodal (Thomasma et al. 1991). In the last 2 decades, habitat-suitability models derived from statistical analysis of distributional datasets have increasingly supplanted the use of conceptual models. When applied in the context of broad-scale planning, wildlife-distribution models typically require input of presence-absence data (derived from systematic regional surveys or compiled from nonsystematic surveys) measured at the patch or site scale, and environmental covariates mapped across the landscape using a geographic information system (GIS). Uncertainty of a single model is assessed using standard metrics (McCullagh and Nelder 1989), whereas uncertainty inherent in the model-selection process is addressed using model averaging (Burnham and Anderson 2002). The robustness of distribution models can be assessed by using cross-validation techniques (McCullagh and Nelder 1989) or by testing against new data (Carroll et al. 1999). Distribution models play a key role in the planning process both as a tool to identify priority habitats and as input to more complex models (Table

18.1).

Distribution models are commonly based on a form of generalized linear model (GLM) such as logistic regression, which models the relations between a binary response variable (e.g., presence-absence) and environmental covariates (McCullagh and Nelder 1989) (Table 18.1). Generalized additive models (GAM) resemble GLMs, but allow more flexibility in the form of the relations between the response variable and the covariates (Hastie and Tibshirani 1990). Logistic regression and other GLMs are often used to fit resource selection functions (RSFs), which are defined as models that yield values proportional to the probability of use of a resource unit (Boyce et al. 2002). For example, RSFs have been used to model fisher habitat relations in California (Carroll et al. 1999; Davis et al. 2007; Spencer et al. 2011), the Rocky Mountain region (Carroll et al. 2001), and British Columbia (Weir and Harestad 2003) at a range of spatial scales. Models derived from radiotelemetry data were applied to a 1500 km^2 study area (Weir and Harestad 2003), whereas those derived from “found” data (compilations of nonsystematic surveys; Carroll et al. 2001) or regional presence/absence surveys (Davis et al. 2007) were applied at the scale of states or provinces.

A limitation of presence/absence data is that observed nondetections can be attributed either to the true absence of the species or to failure of the survey protocol to detect a species that is present (false or sampling absence). Recently developed methods for occupancy modeling, which allow adjustment for incomplete detection, can increase the generality of models built from presence/absence data (MacKenzie et al. 2006; Slauson et al., this volume). Additionally, absence from a site may be due to factors such as barriers to dispersal, or local extirpation caused by predation or disease. Alternative modeling methods, such as Maxent (Phillips and Dudik 2008), that compare sites with presence to all available sites may be used when absence data is unavailable (e.g., for observational data).

Another limitation of typical RSF modeling techniques is that species distribution data often exhibit spatial structure caused by unmeasured environmental factors and population processes (e.g., dispersal, territoriality) that may result in aggregated distributions of individuals (Beale et al. 2010). If ignored, such spatial structure may lead to models that include spurious covariates and have poor predictive power (Beale et al. 2010). Spatial structure may be incorporated into a distribution model by addition of either a spatially structured covariate or an error term (Beale et al. 2010). The GAM developed by Davis et al. (2007) to model fisher habitat suitability in California incorporated a simple autoregressive term that estimated spatial effects through an additional covariate on the basis of observed presence-absence values at neighboring sites within a spatial neighborhood.

Rather than adding spatial structure as a covariate, Carroll et al. (2010) used a hierarchical Bayesian model to incorporate a spatial random effect term (ρ [rho]), which is estimated by means of an intrinsic conditional autoregressive (ICAR) model in which each spatial effect has a Gaussian distribution centered on the mean of the neighboring values (Latimer et al. 2006). ICAR models simultaneously produce estimates of the effects of environmental variables and spatial random effects, allowing the data to determine the best placement of spatial effects (Carroll et al. 2010). This approach also provides better estimation where response data are missing than is possible with simple autoregressive methods. If the spatial random effect is due primarily to population processes, such as dispersal limitation, evaluating predicted distribution without the spatial term can help identify areas that still contain suitable habitat, but from which a species has been extirpated as a result of historical overexploitation. In Carroll et al.’s (2010) model, predictions that include the spatial effect term highlighted areas currently occupied by fishers in northwestern California and the southern Sierra Nevada. Predictions evaluated without the spatial term identified an additional area in the northern Sierra Nevada (Figure 18.1a).

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<txt>A fisher reintroduction project currently (2011) under way in the northern Sierra Nevada near the potential reintroduction area identified above offers an example of the ability of distribution models to inform restoration efforts (Callas and Figura 2008). The reintroduction feasibility analysis compared predictions from a conceptual model, a GLM-based RSF model, and the spatial GAM model of Davis et al. (2007) to determine which portions of the proposed reintroduction area contained habitat most likely to support a fisher population. All 3 models generally agreed about which sites within the 1500-km^2 analysis area had the highest quality habitat (Callas and Figura 2008); however, even the best habitat within the analysis area was predicted to be of lower suitability than currently occupied areas elsewhere in the region.

Although distribution models can provide useful guidance during the planning stages, reintroduction efforts are ultimately limited by practical constraints. For example, fishers were reintroduced to the northern Sierra Nevada onto industrial timberlands, where logistical and financial support was available (partly because of incentives for industrial timber companies to avoid listing of the species and attendant regulatory restrictions), rather than onto adjacent public forestlands with higher predicted suitability. The reintroduction provided an opportunity to test whether the contrast between modeled habitat suitability and current fisher distribution in the northern Sierra Nevada is due primarily to dispersal limitation or to the effects of unmeasured environmental variables such as forest type, prey abundance, or the presence and abundance of competitors and predators. Persistence of fishers in the northern Sierra Nevada, especially in areas predicted to provide high-quality habitat, would support hypotheses attributing their previous absence to historical extirpation. Conversely, if fishers do not persist or occupy atypical habitats, this would support hypotheses attributing their absence to lack of key habitat requirements that may be poorly represented in existing models.

<A>Models of Habitat and Population Connectivity

<txt>Planners often wish to identify not only highly suitable habitat but also “habitat linkages” that may facilitate natural recolonization of suitable but unoccupied habitat without costly reintroductions. Models that predict dispersal or population connectivity often use distribution models as input (Table 18.1). This assumes that the habitat attributes that allow occupancy of an area will also facilitate dispersal. Connectivity analysis methods also make implicit assumptions about the movement process itself (McRae et al. 2008, Carroll et al. 2011). Although this model-based uncertainty is difficult to quantify, testing against genetic data can increase confidence in the predictions of habitat-based connectivity models (Schwartz et al., this volume).

Least-cost-path models are the most widely applied linkage-mapping method, in part because they are computationally simple and commonly available in GIS software (Singleton et al. 2002). The least-cost path can be modeled as a combination of the attraction to preferred habitats minus energetic and security costs (e.g., due to topography and exposure to roads, respectively) (Beier et al. 2008). Because habitat quality is expressed as the relative cost or distance to traverse a site, least-cost-path methods are equivalently termed shortest-path analyses. One limitation to early applications of the shortest-path method was that the single path identified might have the least total cost-distance but be unrealistic biologically (e.g., if segments of the path traversed developed areas). More recent applications of shortest-path analyses to coarse-scale planning problems have broadened the focus to identify a set of near-optimal paths rather than a single path (Theobald 2006; Beier et al. 2008).

Current-flow models, which are based on the design of electrical circuits, are similar in concept to shortest-path models but have a greater capacity to identify the contributions of multiple linkages (McRae et al. 2008; Newman 2010). These methods treat landscapes as conductive surfaces (i.e., networks of nodes connected by resistors) and represent individuals as random walkers that choose to move along edges at probabilities proportional to edge weights. Because the importance of any 1 linkage in a network is affected by the availability of alternative pathways, a change in 1 portion of the landscape affects the inferred importance of all others.

Although both shortest-path and current-flow models are most commonly used to map linkages between a single pair of patches, centrality metrics can also be used to map linkages across the landscape. Centrality metrics consider the role of a node (i.e., a patch or site) in mediating flow between all other nodes in the landscape (i.e., as “gatekeepers” for functional connectivity) (Borgatti 2005). Because centrality metrics reflect potential linkages between all node pairs, they avoid the necessity for *a priori* identification of corridor endpoints. For example, “shortest-path betweenness-centrality” identifies the 1 or several shortest paths that connect each pair of nodes on a graph, and counts the number of such shortest paths in which a node participates (Newman 2010). The loss of a node lying on a large proportion of the shortest paths in the network would disproportionately lengthen distances or transit times between nodes. Like shortest-path corridor-mapping methods, shortest-path betweenness-centrality methods are based on the assumption that the dispersing individual has complete knowledge of the landscape and will choose optimal paths (Freeman 1977). Current-flow (or random-walk) betweenness-centrality assesses the centrality of a node by how often, summed over all node pairs, the node is traversed by a random walk between 2 other nodes (Newman 2010). Thus, this metric counts all paths between nodes, not just the shortest, and is analogous to the behavior of electrical flow in circuits (McRae et al. 2008).

To demonstrate the type of information provided by shortest-path and current-flow betweenness-centralities, we applied these metrics to analyze habitat connectivity for the fisher in California using the Connectivity Analysis Toolkit software (Carroll 2010, Carroll et al. 2011). The input habitat data were based on predicted fisher habitat suitability without the spatial-effect term from Carroll et al. (2010). Shortest-path betweenness-centrality identified a skeletal network of linkages connecting the range of the fisher in California, with a key linkage area connecting northwestern California to the northern Sierra Nevada (Figure 18.1b). Current-flow betweenness-centrality identified a “pinchpoint” of high centrality from the northern Sierra Nevada reintroduction area southward to currently occupied range in the southern Sierra Nevada (Figure 18.1b). This highlights the complementarity of shortest-path betweenness-centrality, which maps a complete network throughout both core and peripheral areas, and current-flow betweenness-centrality, which highlights only the areas where connectivity is important but challenging to maintain. The general outlines of the linkage are not surprising, given that fisher habitat in the Sierra Nevada lies primarily in a restricted band of mid-elevation forest along the western slope of the range (Spencer et al. 2011). The finer-scale pattern of current flow may be useful for establishing conservation priorities within the mid-elevation zone.

When interpreting current-flow output, planners should note that areas with high current values represent pinchpoints of constrained connectivity (i.e., the best among limited options) and not necessarily highly suitable habitat. Such habitat-based linkage maps should be seen as hypotheses to be tested using empirical data on dispersal movements and genetic population structure (Schwartz et al., this volume). Alternatively, a graph network constructed using genetic distances can be tested against habitat data; for example, Garroway et al. (2008) constructed a graph based on genetic data from Ontario fishers. The authors found that node-centrality was negatively related to both the proportion of immigrants in a node and snow depth, suggesting that central nodes were demographic sources located in areas with favorable snow conditions.

<A>Spatially Implicit Dynamic Models

<txt>In the 1990s, the legal and policy debate over the northern spotted owl (*Strix occidentalis caurina*) focused attention on the effects of demographic and environmental stochasticity on long-term population viability (Lamberson et al. 1994). Static habitat-suitability models, such as those described above, may identify factors that affect viability deterministically (e.g., habitat loss), but typically do not provide information on viability thresholds below which a small population may go extinct due to stochastic factors, even when suitable habitat is available (Caughley 1994).

Nonspatial and spatially implicit population-viability models analyze such stochastic factors by combining demographic parameters with simplified representations of landscape pattern and structure (Lamberson et al. 1994). Although fishers and martens are relatively well-studied compared with most vertebrate species, demographic parameters in such models must often be estimated using data from other regions or with educated guesses. Nonetheless, nonspatial viability models assist planners by exploring the behavior of small populations and deriving conclusions that may be generalizable to other regions and contexts (Powell et al., this volume). For example, Lacy and Clark (1993) used VORTEX software to generate insights about viability thresholds for small marten populations. VORTEX can incorporate information on carrying capacity and patch isolation derived from the mapped distribution of available habitat, but lacks the topological information (e.g., patch shape) contained in spatially explicit population models (Lacy et al. 2005).

Schneider and Yodzis (1994) developed a pseudospatial model for Newfoundland martens (*M. a. atrata*) that used the concept of "optimum territory size" to evaluate the potential influences of spatial dynamics (i.e., habitat quality and heterogeneity) on energy balance and reproductive output. As prey abundance and/ or habitat area decreased, martens in the model increased their territory sizes and associated energy costs, resulting in lower fecundity. Scenarios of population extinction resulted from both deterministic factors (e.g., negative growth rate, habitat loss) and stochastic risks to marginally viable populations. These results confirmed those from earlier nonspatial models (Lacy and Clark 1993), providing a means of linking changes in habitat area and pattern to demographic parameters. A subsequent spatially explicit model predicted marten distribution and viability under varying habitat scenarios (Schneider 1997).

<A>Spatially Explicit Dynamic Population Models

<txt>Spatially explicit population models (SEPMs) are a class of simulation models that are both individual based and capable of retaining spatially explicit information on available habitat conditions (DeAngelis and Gross 1992). These models track the fates of many individuals through time as they move across a grid of cells, age, reproduce, and die. The behavior of large numbers of individuals collectively determines the aggregate characteristics that form the model output. SEPMs span a range of complexity, depending on the degree of biological realism and number of demographic parameters they incorporate. Model output may include the mean

population size, mean time to extinction, or the percentage of suitable habitat occupied. Because these models can incorporate habitat-specific demographic parameters, the development of SEPMs has allowed data gathered from intensive demographic studies to be combined with GIS maps of landscape composition and pattern in dynamic models (Murphy and Noon 1992).

PATCH, the SEPM used in both the case studies presented below (Lewis and Hayes 2004; Spencer et al. 2011), links the survival and fecundity of individuals or groups of animals to GIS data on mortality risk and habitat productivity at the scale of an individual or pack territory (Schumaker et al. 2004). Territories are allocated by intersecting the GIS data with an array of hexagonal cells. The different habitat types in the GIS maps are assigned weights based on the relative levels of fecundity and survival expected in those habitat types. Base survival and reproductive rates, derived from published field studies, are then supplied to the model as a population projection matrix. Data are rarely sufficient to build empirical models of the relations between habitat and demography; thus, these steps typically involve subjective judgments whose effect should be evaluated with sensitivity analyses. The model scales these base matrix values using the habitat weights within each hexagon, with lower means translating into lower survival rates or reproductive output. Each individual in the population is tracked through a yearly cycle of survival, fecundity, and dispersal events. Adult organisms are classified as either territorial or floaters. The movement of territorial individuals is governed by a parameter for site fidelity, but floaters must always search for available breeding sites. Movement decisions use a directed random walk that combines varying proportions of randomness, correlation, and attraction to higher quality habitat (Schumaker et al. 2004). HEXSIM, the successor to PATCH, provides additional analytical capabilities (www.hexsim.net; Heinrichs et al. 2010).

Parameterizing SEPMs requires the input of both predictions from a distribution model (habitat maps) and data on demographic rates (e.g., survival and fecundity in different habitat types). Although uncertainty in such models is difficult to quantify because of the large number of parameters involved, sensitivity analysis can be used to evaluate the robustness of model output to variation in input parameters (Spencer et al. 2011). If SEPM results are considered in the proper context, they have the potential to offer insights into both spatial and nonspatial factors that might influence the success of reintroduction and other conservation efforts. For example, SEPMs, like RSF models, may suggest which areas hold habitat that can support reintroduced populations and, like VORTEX, may suggest the minimum number of individuals to release to ensure a high probability of reintroduction success (Carroll et al. 2003b).

<B>Case Study 1: Using a Dynamic Population Model to Evaluate the Feasibility of Reintroducing Fishers to Washington State

<txt>The feasibility assessment preceding the recent fisher reintroduction in Washington state provides an example of the use of SEPM (Lewis and Hayes 2004). A conceptual habitat model was developed to map potentially suitable habitat throughout the Olympic Peninsula and Cascade Range in western Washington, USA; both regions were within the historical range of the fisher and still supported extensive areas of late-successional conifer forests (Figure 18.2). Because the fisher was extirpated from Washington by the mid-1900s, little site-specific ecological or demographic information was available to quantitatively assess habitat availability for a reintroduced population. Consequently, the habitat model developed by Lewis and Hayes (2004) was based on fisher-habitat associations reported in the literature (e.g., Buskirk and Powell 1994; Powell and Zielinski 1994; Weir and Harestad 2003). The habitat suitability model included 4 variables (percent vegetation cover, percent conifer cover, quadratic mean diameter of

overstory trees, and elevation) to identify relatively dense, late-successional forests at low and mid-elevations (Lewis and Hayes 2004). The study also identified suitable travel cover for fishers (low- and mid-elevation mid-seral forest) and mapped the distribution of suitable habitat and travel cover. The 3 largest blocks of interconnected suitable habitat and travel cover were identified as potential reintroduction areas: Olympic Peninsula, southwestern Cascades, and northwestern Cascades (Figure 18.2).

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<txt>Lewis and Hayes (2004) used 6 criteria to rank the suitability of these 3 areas for fisher reintroduction: amount of suitable habitat, amount of suitable habitat on public land, amount of suitable habitat in protected areas (National Parks, National Monuments, and Wilderness Areas), amount of land with >50% suitable habitat, proximity to an existing fisher population, and estimated fisher carrying capacity. The authors used a GIS to calculate the first 5 criteria, and PATCH to estimate carrying capacity for each potential reintroduction area (Lewis and Hayes 2004). They then used PATCH output to compare relative carrying-capacity estimates among areas, rather than to predict absolute carrying capacities. PATCH simulations incorporated a habitat map and suitability scores for 7 habitat types (Lewis and Hayes 2004). The authors based suitability scores on a scale of 0–10, with 0 being given to those cover types considered nonhabitat (e.g., water, urban) and 10 to cover types considered optimal habitat. Because fishers select late-seral forests at the stand scale and use structural elements typically found in late-seral stands for den and rest sites, the authors considered the late-seral forest cover type to be optimal habitat. The authors considered mid-seral forests to be intermediate in habitat suitability and early seral forests to have low suitability. Habitat scores also differed with elevation (above and below the Pacific silver fir [*Abies amabilis*] zone).

The authors assessed uncertainty in model outputs using sensitivity analyses performed with 3 estimates of dispersal distances and 3 Leslie matrices of survival and fecundity values (Lewis and Hayes 2004). They also used an alternative set of habitat scores in the sensitivity analyses that assigned lower values to suboptimal habitat types. Elasticity analyses indicated that results from all parameter sets (matrices with low, mean, and high values for survival and fecundity) were most sensitive to adult female survival, followed by juvenile survival, and then equally by subadult survival and adult female fecundity. PATCH simulation output was highly sensitive to assumptions concerning the contrast between optimal and suboptimal habitat types, but relatively insensitive to alternative assumptions about dispersal distances (Lewis and Hayes 2004).

The Olympic Peninsula was chosen as the best location for the first fisher reintroduction in Washington because it ranked first in 5 of 6 suitability criteria. Although the Olympic Peninsula ranked third in distance from an existing fisher population, the static habitat-suitability model suggested that the area supported the greatest amount, best configuration, and greatest protection of suitable habitat among the 3 potential reintroduction areas (Figure 18.2). The PATCH model simulations also indicated that the Olympic Peninsula supported a significantly greater carrying capacity than the 2 Cascade areas. Support from a key land-management agency (Olympic National Park) also motivated selection of this reintroduction area.

The 49 fishers released during late 2008 and early 2009 traveled extensively after being released and are currently distributed broadly across diverse landscapes, including lands previously classified as both suitable and unsuitable in the feasibility assessment (Lewis and Hayes 2004; Lewis et al. 2010). Altogether, 90 fishers were released from 2008 to 2010, but many translocated fishers have not yet established home ranges and formal analyses are not yet possible. Researchers are currently monitoring home-range establishment by translocated fishers on the Olympic Peninsula, but a comprehensive assessment of the accuracy of the suitability model will not be possible until longer-term occupancy of home ranges is assessed over the next decade.

Without region-specific data to evaluate the feasibility of a reintroduction, managers must rely on data from other areas. Additionally, like most geographically extensive models, the Washington state habitat model did not include inputs for forest-floor structure (e.g., downed logs, slash and cull piles) or prey abundance and distribution, which are likely to be important predictors of fisher occupancy on the Olympic Peninsula. This points to the challenges of extrapolating habitat models developed from data on extant populations to new areas that may contain very different prey and vegetation communities. Although the assessment of suitable habitat for fishers was limited by an incomplete understanding of fisher habitat requirements in the coastal Pacific Northwest, the models provided useful tools to evaluate and draw informed conclusions about the feasibility of a successful reintroduction based on the best available information.

<B>Case Study 2: Using Coupled Dynamic Habitat and Population Models to Evaluate Fisher Conservation Strategies in the Southern Sierra Nevada

<txt>An important limitation of most habitat models for *Martes* is that they predict suitability based on a static “snapshot” of current vegetation conditions. Consequently, some planners have sought to project how such vegetation attributes may change over time to better predict long-term habitat suitability. The accelerating pace of anthropogenic climate change (Lawler et al., this volume) is an additional motivation for analyzing habitat conditions in a

dynamic model. To address these issues, Spencer et al. (2011) used coupled dynamic habitat and population models to project the potential effects of alternative management strategies (e.g., landscape-level fuels treatments) on the southern Sierra Nevada fisher population. This study was among the first to integrate many of the modeling approaches described above into a single decision-support process.

Spencer et al.’s (2011) analysis area supports the southernmost population of fishers, consisting of a few hundred individuals in the southern Sierra Nevada of California that are isolated from other populations by >400 km (Zielinski et al. 2005) (Figure 18.3). Several studies have projected future increases in wildfire intensity and extent in this region (Miller et al. 2009; Westerling et al. 2009), motivating proposals for vegetation management (e.g., forest thinning) to alter wildfire behavior (U.S. Department of Agriculture 2004). Such actions may also reduce fisher habitat quality and continuity, at least in the short term, because fishers select the densest forest stands as resting habitat (Zielinski et al. 2004a). To assess the status of the population and evaluate alternative vegetation-management approaches, Spencer et al. (2011) coupled a fisher SEPM with other spatially explicit models. The coupled models allowed the authors to test alternative hypotheses in a simulation environment, evaluate the relative risks of fuels treatments and wildfires to the population, and identify conservation actions that are likely to sustain and expand the population (Spencer et al. 2011).

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<txt>Spencer et al. (2011) built a number of alternative GAM models using GIS data layers and fisher detection-nondetection data from a regional systematic monitoring program (Zielinski et al. 2006c). The best GAM model provided a strong fit to the fisher data using 3 predictors: latitide-adjusted elevation, annual precipitation, and total aboveground biomass of

trees (kg/ha) averaged over 5 km^2 (see Spencer et al. 2008). The model suggested that fishers in the southern Sierra Nevada are associated with mid-elevation forests that experience relatively low annual precipitation and support abundant large trees. Forest biomass provided the best discrimination of fisher occupancy among the biotic variables tested, probably because it correlates strongly with many forest-structure variables known to predict fisher habitat selection at finer spatial scales (e.g., large trees, dense canopies, abundant dead-wood structures) (Zielinski et al. 2004a,b; 2006c).

Spencer et al. (2011) then parameterized the PATCH model using predicted probability of fisher occurrence from the GAM to estimate an equilibrium fisher population size (or carrying capacity) and to identify potential population source, sink, and expansion areas. Each territory was assigned a score from 0 to 10 in PATCH, based on mean occupancy scores within the territory. High-quality territories (territory score >7.5, reflecting an average within-territory occupancy >0.75) were assigned high fecundity and survivorship rates based on a 4-stage Leslie matrix and demographic rates from Lewis and Hayes (2004). Below the maximum score of 7.5, fecundity and survival rates were decremented linearly with territory score. The average resulting lambda (intrinsic rate of population growth) for territories scoring >7.5 was 1.19 (i.e., predicted source territories); lambda for territories scoring about 6.0–7.0 averaged about 1.0 (stable population); and lambda for territories scoring less than about 5.5 averaged <1.0 (predicted sink territories) (Spencer et al. 2011). Despite assumptions about linear correlations between fisher vital rates and predicted occupancy (from the GAM), the SEPM parameters, when combined with appropriate sensitivity analyses, were judged useful for estimating potential equilibrium population sizes and for relative comparisons between alternative forest-management scenarios. Fishers were initially seeded into the highest-scoring territories and those where fishers were detected in the monitoring data. After the SEPM was run for 40 years to allow the model population to reach equilibrium on the landscape, the ending population size was recorded as a measure of carrying capacity for comparisons among different scenarios. The authors compared scenarios using equilibrium behavior (e.g., ending population size) rather than transient dynamics (e.g., temporal trends) because the latter metrics are typically more sensitive to uncertainty in model parameters (Grimm and Railsback 2005). Model uncertainty was assessed using a sensitivity analysis that varied vital rates, territory sizes, initial population sizes, maximum dispersal distances, and other model parameters. Population dynamics were highly sensitive to adult female survivorship and relatively insensitive to other age-specific vital rates. Territory size had a greater effect on estimated carrying capacity than did initial population size or dispersal distance (Spencer et al. 2011).

The southern Sierra Nevada fisher population is generally restricted to habitats south of the Merced River, despite some apparently suitable habitat to the north (Figure 18.3). Spencer et al. (2011) estimated carrying capacity in the area occupied currently by constraining the model fishers from establishing territories north of the river. To evaluate the potential for northward expansion under current habitat conditions, the authors then allowed fishers to establish territories north of the river. Because there is evidence of elevated human-influenced mortality rates in the northern portion of the occupied range (e.g., roadkill, diseases spread by cats and dogs), the analysis then decreased survivorship in 5% increments throughout the entire analysis area to observe effects on the modeled population expansion.

Using the most defensible range of input parameters, the SEPM results estimate the equilibrium population size at 73–147 adult females south of the Merced River (Figure 18.3). After weighing various uncertainties in these estimates and comparing them with several independent estimates (based on density extrapolations from fisher field studies and sampling theory applied to the regional fisher monitoring data), the authors estimated that the current population is most likely between 160 and 360 individuals, and includes only about 55–120 adult females.

When modeled fishers were allowed to cross the Merced River, the population expanded northward into mostly moderate-value habitat, establishing modest new population source areas north of the Tuolumne River. The expansion front stalled about 90 km north of the Merced River, where predicted probability of fisher occurrence generally dropped below 0.5. Predicted territory occupancy north of the Merced River dropped with decreasing survivorship rates, with no expansion north of the Tuolumne River when the survival rates were reduced by 15%, and no expansion north of the Merced River when survival rates were reduced by 20%.

To evaluate how fires, vegetation management, and other disturbances might affect the population, Spencer et al. (2011) coupled the spatially explicit habitat and population models with a stochastic, spatially explicit landscape-change model, LANDIS-II (Mladenoff 2004; Scheller et al. 2007). LANDIS-II simulates how succession, fires, forest management, and other processes may affect forest vegetation over time by tracking changes in forest biomass by tree species and age cohorts. Using a factorial experimental design with replication, the authors used LANDIS-II to simulate vegetation for 50 years in a variety of scenarios. These scenarios assumed 2 alternative future fire regimes (1 calibrated to match recent fire histories, and 1 that assumed more severe fire conditions in the future) and different types, rates, and locations of fuels treatments. For each decade and replicate, the forest-biomass outputs from LANDIS-II were used to update the habitat model on which PATCH runs. The model did not simulate direct mortality of fishers due, for example, to wildfire, but fishers could disperse to higher suitability areas in the event a fire or management action reduced the habitat value of their current territory. Model fishers unable to settle into unoccupied, high-quality territories following a disturbance event would experience relatively low survival and fecundity rates, as appropriate for the value of the particular territory where they settled. Scenarios were compared using total female population size at year 60. Structural-equation models were used to assess the net effects of fuels treatments on fishers, which can include direct negative effects (removal of forest biomass by logging) as well as indirect positive effects (by limiting fires that also remove biomass).

Model results suggested that, across a range of alternative fire regimes and vegetation treatments, the positive indirect effects of fuels treatments on fishers generally outweighed the direct negative effects. However, coarse-resolution landscape and fuels models, such as those used in this study, more accurately project changes in fire extent than in fire severity, yet the latter factor may have a greater impact on fisher habitat suitability. Spencer et al. (2011) did not use a formal population-viability analysis to estimate level of risk (e.g., probabilities of extirpation); however, the relatively small size of the southern Sierra Nevada fisher population, at <400 individuals, suggests that it may be at risk of extirpation due to stochastic threats. Northward expansion of the population appeared to have the greatest potential to increase the population’s size and viability. Population expansion could be facilitated by (1) forest-management activities in the area north of the Merced River that increase fisher habitat quality and contiguity, and (2) adaptive management in the northern portion of the current range (in and immediately south of Yosemite National Park), to reduce fisher mortality sources and increase survivorship. The authors concluded that fuel treatments strategically located in and adjacent to areas with the greatest risk of severe crown fires, based on evaluation of human ignition sources and fuels characteristics, could also reduce risks to fisher habitat quality.

<A>Multispecies Models

<txt>Although legal mandates often focus on conservation of individual species of concern, single-species conservation planning may often lead to less efficient solutions than an approach that simultaneously addresses the habitat needs of many species of concern (Marcot and Raphael, this volume). Several software packages (e.g., MARXAN [Ball et al. 2009], ZONATION [Moilanen et al. 2009]) are commonly used to analyze output from distribution models to find solutions (i.e., landscape designs) that optimally (e.g., in the minimum area) capture habitat needs for many species. Because most real-world optimization problems are too complex to be solved exactly, reserve-selection models identify both an approximation of the "best" solution and the degree of variation (or uncertainty) among alternative approximations (Ball et al. 2009). MARXAN has been used to assess the overlap and contrasts between the habitat requirements of *Martes* species and those of other taxa in the Rocky Mountain region and in California, USA (Carroll et al. 2003a; Zielinski et al. 2006a).

Although these studies addressed spatial relations among habitat conditions for multiple species, it is more challenging to project how *Martes* populations will interact dynamically with populations of potential prey or predator species. Using the ZONATION software, Rayfield et al. (2009) developed a conservation plan for the American marten in an area of Quebec, Canada that considered the spatial interaction between the distribution of the marten and its 2 primary prey species. Areas were identified providing suitable habitat for all 3 species and of sufficient area and connectivity for marten population persistence. As yet, no studies have projected the indirect effects of climate change on *Martes* populations via changes in vegetation and disturbance patterns, although these have recently been completed for other taxa (Keith et al. 2008).

<A>Use of Models within the Conservation Planning Process

<txt>The 4 types of models reviewed above (predicting distribution, dispersal, persistence, and optimal reserves; Table 18.1) have distinct roles within conservation-planning processes for *Martes*. Distribution models in some form are used to support almost all planning efforts attempting to integrate *Martes* conservation into land-management practices (Lofroth et al. 2011). The relevance of the remaining model types varies depending on available data and the goals of the planning process. Connectivity or dispersal is rarely addressed in planning for *Martes* or other wildlife populations because of limited availability of dispersal data and limited understanding of the influence of dispersal processes on population persistence. New techniques for analysis of genetic data may allow connectivity to be assessed more rigorously in the planning process (Schwartz et al., this volume).

Because the ultimate goal of *Martes* conservation is population persistence, one might anticipate broad use of viability models such as SEPM (Schumaker et al. 2004). The limited availability of demographic data, and the uncertainty associated with using demographic parameters from other populations, however, have limited the application of such complex models in planning processes. Recent examples (e.g., Spencer et al. 2011) where such models were developed, evaluated with detailed sensitivity analyses, and applied to management issues may encourage their broader use in planning. The key to appropriate use of such complex models is to assess what qualitative insights are robust to the many potential sources of uncertainty.

<A>Conclusions

<txt>The relatively large territory sizes and habitat-limited dispersal ability of most

Martes species suggest that their persistence may be influenced by large-scale population processes, as is true for other forest-associated “focal” species, such as the Northern Spotted Owl (Thompson 1991; Lamberson et al. 1994). In contrast to findings about the spotted owl, several studies suggest that habitat requirements for the fisher in western North America are complex and poorly described by broad-scale GIS layers for such attributes as forest type and age class (Davis et al. 2007; Carroll et al. 2010). Fisher-habitat models with a relatively large proportion of unexplained variance, or that contain covariates that are surrogates for unmeasured factors, will have poor generality when extrapolated to other areas (Carroll et al. 1999). When this problem is combined with the challenge of representing large-scale population processes accurately in a simulation model, it is clear that the predictions of quantitative habitat and viability models will be highly uncertain. Additionally, the examples discussed in this review suggest that the link between the results of such models and management is often mediated by the many factors that constrain management decisions. Nevertheless, the costs associated with reintroductions and other broad-scale conservation efforts generally justify the use of such models to inform the planning process before substantial resources are committed. The complexity of conserving *Martes* populations, given increasing human demands on forest ecosystems, suggests that quantitative models will be increasingly relevant for enhancing the success of *Martes* conservation efforts, as long as model uncertainty is considered explicitly and model results are used to inform decisions rather than predict outcomes.

<A>Acknowledgments

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Table 18.1. Types of habitat and viability models discussed in this chapter

Model type	Acronym	Input data	Output predictions	Reference
Habitat suitability index	HSI	Environmental	Distribution	Thomasma et al. 1991
Generalized linear	GLM	Environmental	Distribution	Carroll et al. 1999
Generalized additive	GAM	Environmental	Distribution	Davis et al. 2007
Hierarchical Bayesian spatial	HB	Environmental	Distribution	Carroll et al. 2010
Centrality		Habitat	Dispersal	Garroway et al. 2008
Non-spatial viability		Habitat, demographic	Persistence	Lacy and Clark 1993
Spatially explicit population	SEPM	Habitat, demographic	Persistence	Spencer et al. 2011 Lewis and Hayes 2004
Reserve selection		Distribution	Optimal reserves	Zielinski et al. 2006a

Figure 18.1. Use of a hierarchical spatial model and centrality analysis to evaluate fisher distribution and population connectivity in California. (a) Spatial model predictions of Carroll et al. (2010) identify currently occupied areas (composite prediction), as well as areas of potentially suitable habitat that may be unoccupied currently because of dispersal limitations (prediction without rho). (b) Shortest-path and current-flow betweenness centrality was then used to predict habitat linkages that might provide dispersal routes between populations.

Figure 18.2. The 3 areas in western Washington state that were compared to evaluate their capability for supporting a reintroduced fisher population. Areas of suitable habitat >3000 ha are shown. Fishers were released onto the Olympic Peninsula beginning in 2008.

Figure 18.3. Influence of survival rate on modeled fisher source-sink dynamics and potential for population expansion north of the Merced River (dashed line). Net value of territories (annualized births minus deaths) were averaged across 20 replicate simulations run for 200 years using intermediate parameter values. Source territories (births exceed deaths) are shaded, and sink territories (deaths exceed births) are hatched. The inset illustrates the reduced potential for northward expansion and establishment of new source territories with a 10% reduction in survivorship relative to baseline assumptions. Data gaps caused underrepresentation of territory value in Sequoia-Kings Canyon National Park. Adapted from Spencer et al. (2011).

Figure 1a.

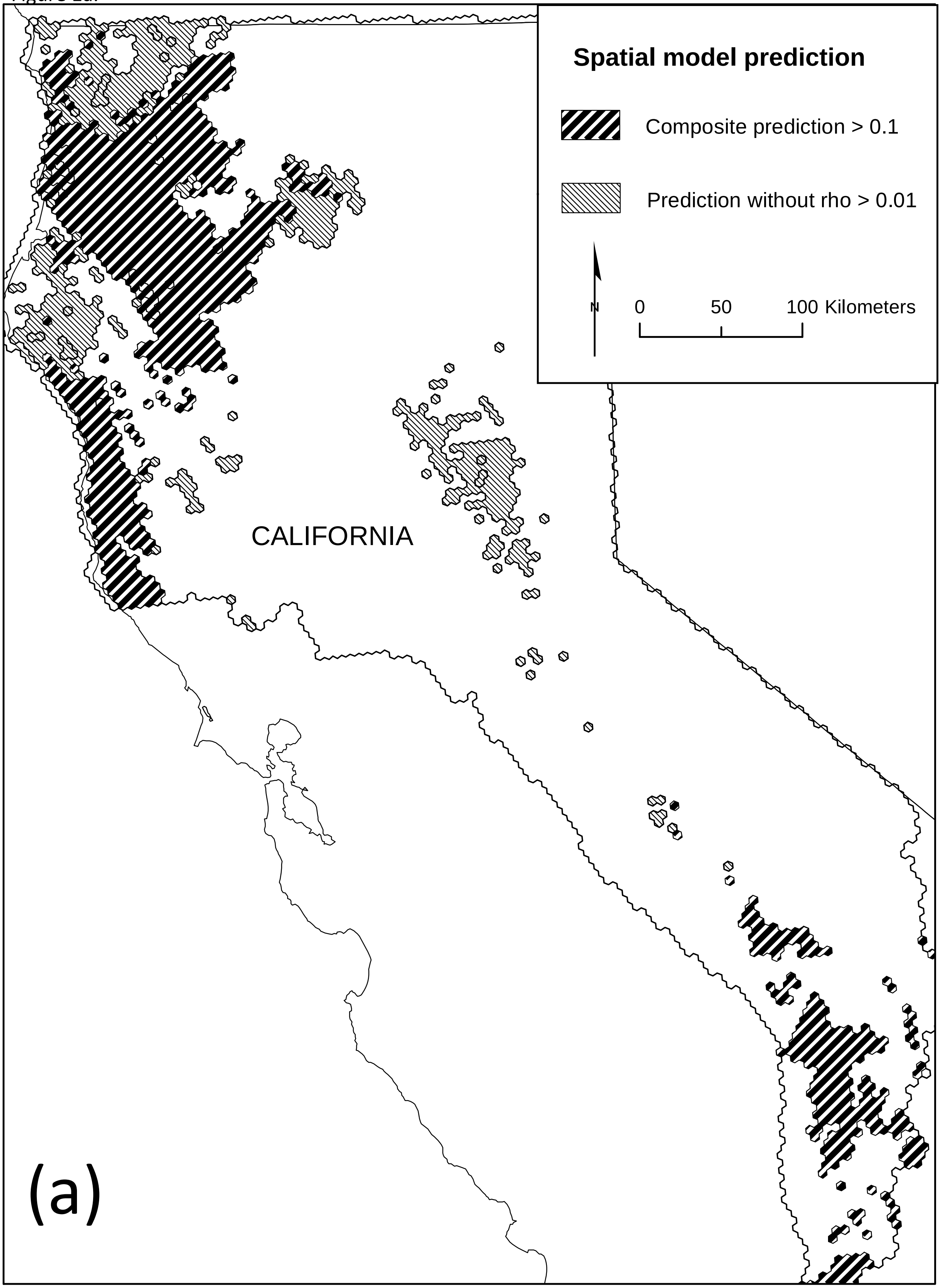
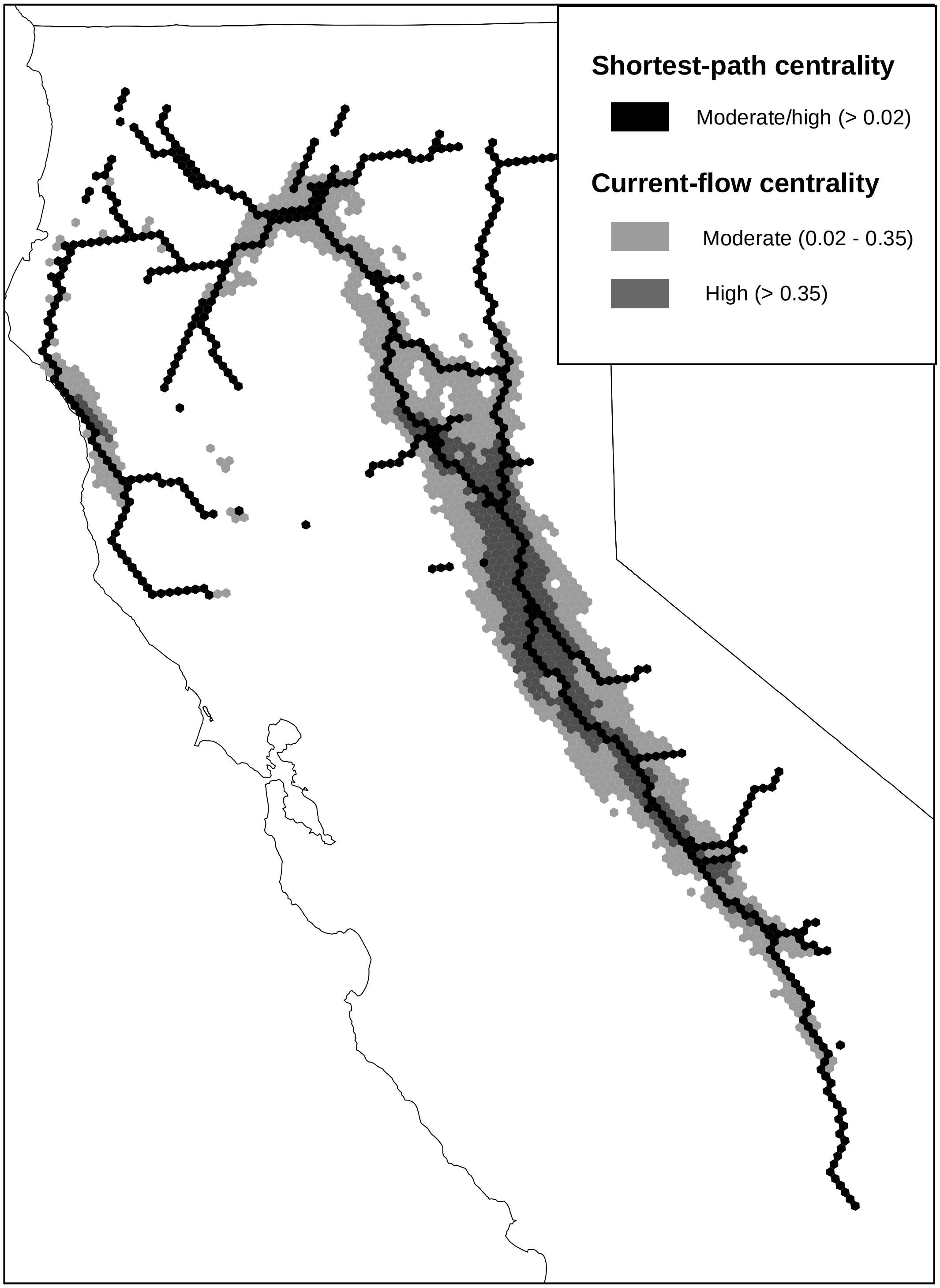
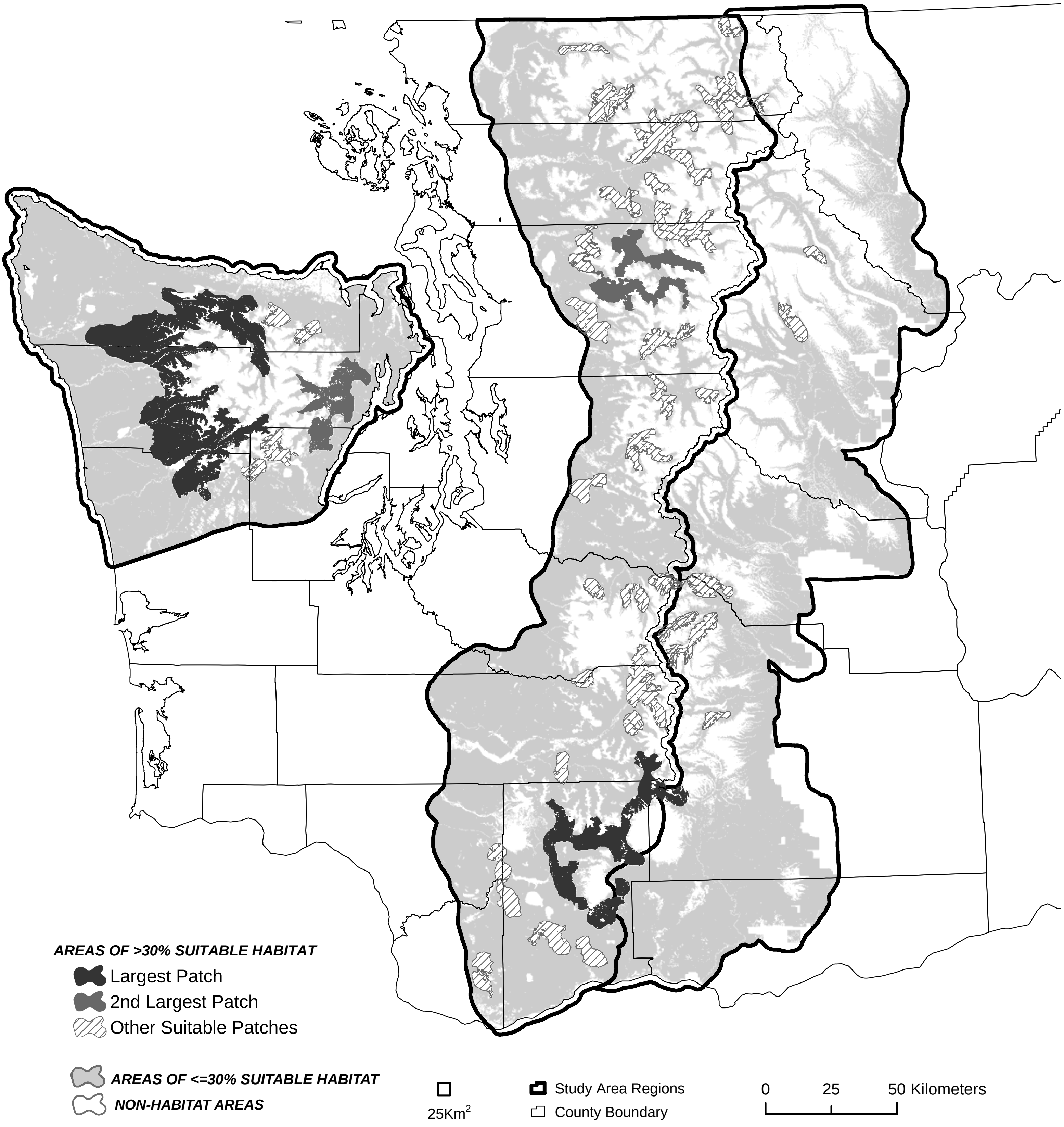
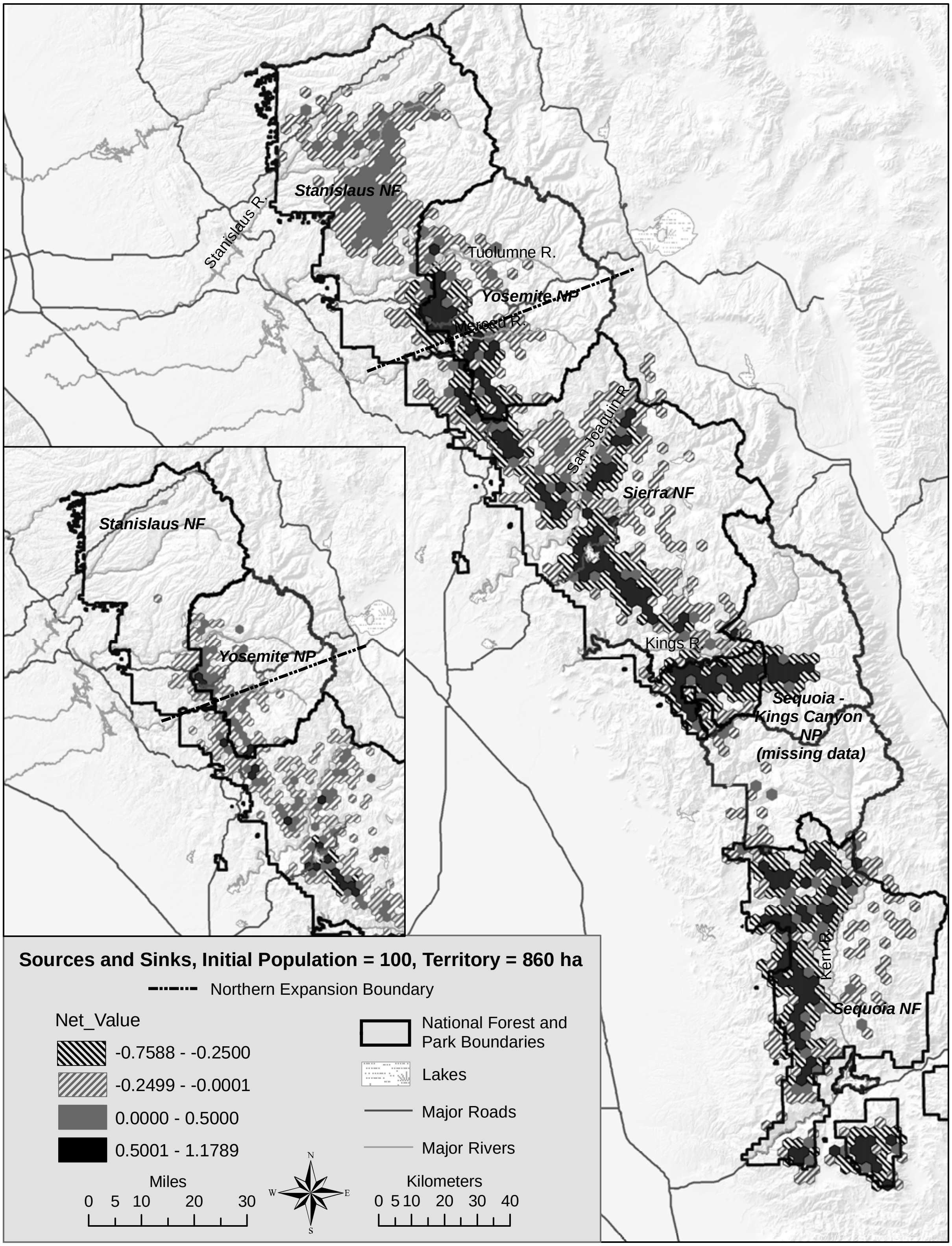

Spatial model prediction
▨ Composite prediction > 0.1
▨ Prediction without rho > 0.01
N
0 50 100 Kilometers
CALIFORNIA
(a)

Figure 1b.


Shortest-path centrality
Moderate/high (> 0.02)
Current-flow centrality
Moderate (0.02 - 0.35)
High (> 0.35)


AREAS OF >30% SUITABLE HABITAT
Largest Patch
2nd Largest Patch
Other Suitable Patches
AREAS OF <=30% SUITABLE HABITAT
NON-HABITAT AREAS
25Km2
Study Area Regions
County Boundary
0
25
50 Kilometers



Stanislaus NF
Stanislaus R.
Tuolumne R.
Yosemite NP
Merced R.
San Joaquin R.
Sierra NF
Kings R.
Sequoia - Kings Canyon NP (missing data)
Kern R.
Sequoia NF
Stanislaus NF
Yosemite NP
Sources and Sinks, Initial Population = 100, Territory = 860 ha
Northern Expansion Boundary
Net_Value
-0.7588 - -0.2500
-0.2499 - -0.0001
0.0000 - 0.5000
0.5001 - 1.1789
National Forest and Park Boundaries
Lakes
Major Roads
Major Rivers
Miles
0 5 10 20 30
N
W
E
S
Kilometers
0 5 10 20 30 40

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