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# Using landscape suitability models to reconcile conservation planning for two key forest predators

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ABSTRACT

Protection of area-limited species is an important component of plans to conserve biodiversity, but the habitat needs of such species can be different and important habitats may not align with existing reserves. We used empirically derived landscape suitability models for the spotted owl and the fisher to evaluate the overlap in habitat suitability for these two old forest-associated predators in an area of northern California affected by the Northwest Forest Plan (NWFP), a bioregional conservation plan. The area includes designated Wilderness areas and new reserves (Late-Successional Reserves, LSRs) established under the NWFP. We used the site selection algorithm MARXAN to identify priority habitat areas for each species, and for both combined, and to compare these areas with reserves. Sites were selected under two constraints, to achieve a threshold proportion of total habitat value and to select new areas equal to the total current area in existing reserves. The rank correlation between predicted value for the two species was low (0.11), because areas of highest predicted habitat value were more widely distributed for the owl. This difference also meant that the sites selected to optimize habitat value were more aggregated for fishers than owls, resulting in greater overlap of owl habitat and current reserves. To capture 25%, 50% and 75% of total habitat value for the owl required 14.0%, 29.2%, and 47.3% of the planning units, respectively; capturing the same for the fisher required only 5.3%, 13.5%, and 27.2%. A combined owl-fisher scenario resulted in areas that overlapped only ~50% of existing reserves. The current location of LSRs may not be the best solution to maintaining well-connected habitats for these area-limited species in northwestern California. Whether LSRs are a better solution to protecting the diversity of other lesser-known taxa (i.e., salamanders and mollusks) is the subject of related work.



## 1. Introduction

Conservation of area-limited species (*sensu* Lambeck, 1997) is one avenue to attempt to protect other species with which they share habitat and to protect the structures and ecological functions that sustain them (Noss and Cooperrider, 1994). The spotted owl (*S. occidentalis*) and the fisher (*Martes pennanti;*) have disproportionately large home ranges (3–10 $km^2$ for the

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spotted owl (Gutiérrez et al., 1995) and 4–90 $km^2$ for the fisher (Zielinski et al., 2004a)), qualifying them as area-limited focal species for conservation planning. The microhabitat and landscape features selected by fishers for resting (Zielinski et al., 2004a; Zielinski et al., 2004b) appear similar to the nest and roost structures used by northern spotted owls (Blakesley et al., 1992; Hunter et al., 1995), but there has been no formal comparison of owl and fisher habitat at any scale of reference. Despite the apparent similarity of their habitat, the spotted owl and fisher differ in their ability to move through fragmented landscapes. Owls are able to move relatively easily between habitat patches and can move more rapidly through or around unsuitable habitat than fishers. Comparing, and then integrating, the landscape habitat needs of these two species, which differ in their vagilities but which share trophic status and habitat association, should result in a more comprehensive application of the area-limited focal species approach than relying on either species alone (e.g., Carroll et al., 2003).

The listing of the northern spotted owl (*S. occidentalis caurina*) in 1990 as "threatened" under the US Endangered Species Act precipitated a political and legal process that resulted in the bioregional land management plan referred to as the Northwest Forest Plan (NWFP; USDA Forest Service and USDI Bureau of Land Management, 1994). Prominent goals of the NWFP were to arrest the loss of old-forest conditions, protect habitat for the spotted owl, and moderate the economic volatility that had occurred in timber-dependent communities within the region. An important component of the plan was to designate Late-Successional Reserves that were well-distributed across the geographic range of the owl and were either in late-successional condition, or would be managed to develop into this condition.

Since the inception of the Northwest Forest Plan, new information has become available about the spatial distribution of owls and their habitat. In the late 1990s, owl survey information was used to develop a spatially explicit empirical habitat suitability model for the owl in northwestern California (Fig. 1, Table 1, Zabel et al., 2003). This model was validated with independent datasets, found superior to the description of habitat used as the basis for the NWFP in California, and was used to predict relative habitat suitability across the range of the owl on four national forests in northern California (Zabel et al., 2003). The map of predicted suitability values has been used by the United States Fish and Wildlife Service (USFWS) to evaluate the effects of proposed stand-altering activities, but it has not been used to identify areas of high habitat value in the region, nor to evaluate the relative habitat value of the Late-Successional Reserve system in California that was established as part of the Northwest Forest Plan.

In 2003 the USFWS decided that the fisher was warranted for federal listing under the Endangered Species Act in California, Oregon, and Washington (US Fish and Wildlife Service, 2003). The fisher, like the owl, is a forest predator associated with late-successional forest conditions (Powell and Zielinski, 1994; Carroll et al., 1999; Zielinski et al., 2004b). During the development of the NWFP, the effects of various alternative land management scenarios on species other than the spotted owl were evaluated by panels of scientific experts. The fisher was identified among the species of mammals with the lowest likelihood of remaining well distributed under the proposed management option (USDA Forest Service and USDI Bureau of Land Management, 1993), but this was due to general uncertainty about its welfare, independent of the management option that was considered (USDA Forest Service and USDI Bureau of Land Management, 1993). Now, however, the precarious status of fishers in the Pacific states is well documented (Zielinski et al., 1995; Aubry and Lewis, 2003; US Fish and Wildlife Service, 2003; Zielinski et al., 2005) making it important to determine how well the system of Late-Successional Reserves, and other land management decisions instituted by the Northwest Forest Plan, serve the fisher's habitat needs.

In 1999, a landscape suitability map for the fisher was developed from an empirical model based on new survey data (Fig. 2, Table 1; Carroll et al., 1999). This model was applied over much the same region as the owl habitat model developed by Zabel et al. (2003). The availability of the new owl and fisher landscape suitability models, each developed from field survey data, tested on independent data, and overlapping the area affected by the Northwest Forest Plan in northern California, provides an exceptional opportunity to evaluate their similarities and differences and to see how they align with the system of Late-Successional Reserves designated by the Northwest Forest Plan. Given the general similarity of these two charismatic species, it is of ecological and conservation interest to determine how their predicted habitat associations differ and whether the provisions of the Northwest Forest Plan help protect the fisher and its habitat. We assume that the Late-Successional Reserve network (largely designed to benefit owls) should do a better job of protecting owl habitat than fisher habitat. The degree to which habitat already protected for the owl serves the habitat needs for fishers will help determine whether the recovery of the fisher will require land allocations or management approaches that appreciably differ from those already prescribed for the owl.

The primary tool in modern multiple-species conservation planning is the reserve selection algorithm, which identifies a network of sites that optimize the conservation of biodiversity within constraints (Margules and Pressey, 2000). The northern spotted owl and fisher ranges overlap throughout much of the forest region of northwestern California (Fig. 3). We evaluated the combination of sites that maximized their combined habitat value of spotted owls and fishers. This 'complementarity' exercise (e.g., Margules et al., 1988; Margules and Pressey, 2000) estimates the gain in representation of habitat value – for each species separately and when they are considered together – when a site or area is added to an existing set of protected areas. We used the site-selection program MARXAN (Ball and Possingham, 2000), which executes the complementarity exercise by comparing outcomes when existing protected areas are either included or excluded in the site-selection process.

Although fishers and spotted owls are archetypal 'area-limited' focal species, relying on only their habitat needs will lead to an incomplete conservation plan (Wilcove and Master, 2005). A comprehensive plan requires meeting the

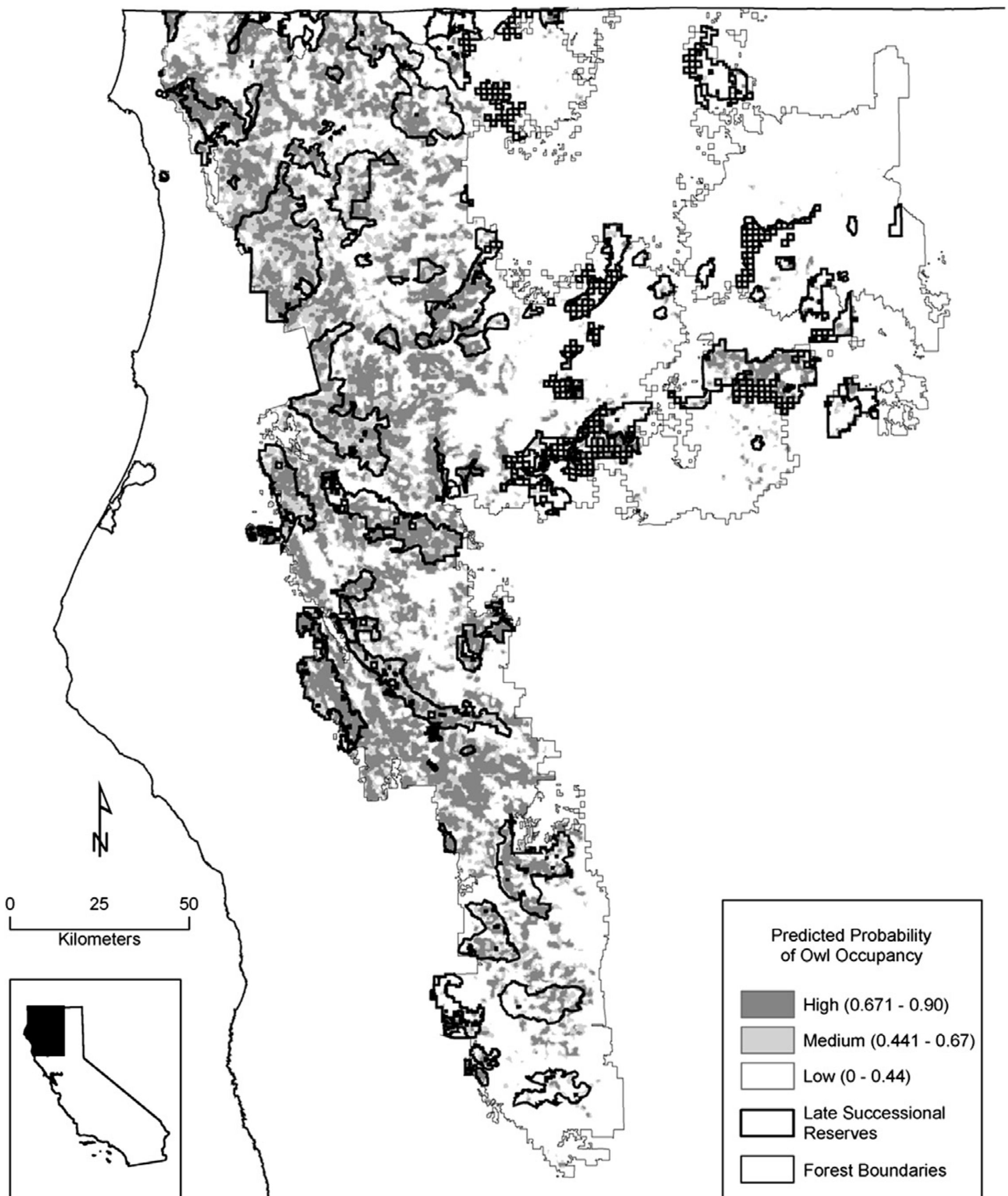


**Fig. 1 – Landscape habitat suitability map for the northern spotted owl in northwestern California (Zabel et al., 2003).**

needs of individual species of conservation interest (i.e., 'fine filters') as well as representing ecological communities in the selected areas (i.e., 'coarse filter'; Noss, 1987). However, the fine filter strategy is typically viewed as requiring the consideration of more than a few focal species. Multiple focal species are necessary to protect the structures and processes that maintain ecosystem function at multiple scales (Lambeck, 1997; Lambeck, 1999; Carroll et al., 2001; Hess and King, 2002). Moreover, landscapes that are suitable for relatively fast-moving or vagile species may not be suitable for slower-moving species or those with short-range dispersal (Matlack and Monde, 2004). A complete set of focal species for the late-successional forest ecosystem would include species that respond to fine-scale environmental gradients, such as species from Lambeck's (1999) 'dispersal-limited' and 'narrowly endemic' categories (Lambeck, 1999) or 'low mobility' species (Matlack and Monde, 2004). Herein we consider the habitat needs of spotted owls and fishers, but we also establish the foundation for subsequent analyses in which we will include a diverse array of taxa in other

**Table 1 – Characteristics of the original fisher (Carroll et al., 1999) and northern spotted owl (Zabel et al., 2003) models that are used here to evaluate existing reserves and to select priority areas for conservation**

| | Fisher (Carroll et al., 1999) | Northern spotted owl (Zabel et al., 2003) |
|---|---|---|
| Predictors in selected model | Moving average (10 $km^2$) of tree canopy closure – moving average of tree size + moving average of percent conifer – annual precipitation + UTM northing – UTM northing$^2$ – moving average tree canopy closure (moving average of percent conifer) + moving average of tree size (annual precipitation) | Log(nesting and roosting habitat) + foraging habitat + foraging habitat$^2$ |
| Extent of area of model application | 67,000 $km^2$ | 22,000 $km^2$ |
| Accuracy/diagnostics | Correct classification (presence and absence):[a] • Development data = 80.4% • Validation data = 71.8% | Correct classification (presence only):[a] • Development data = 93.94% • Validation data; range = 85.19–92.22% for four data sets |

a At optimal cut-point.

focal species categories. We will ultimately consider the habitat of terrestrial mollusks, salamanders, lichens, mosses and fungi. These species were systematically sampled at standard forest vegetation inventory plots in northwestern California (from the nationwide Forest Inventory and Analysis (FIA) system; Roesch and Reams, 1999) and their habitat and distributions have been modeled (Dunk et al., 2004; Welsh et al., 2006; Dunk et al., unpublished data). Thus, the owl and fisher analysis presented here is also the first in a series that will integrate multiple types of focal species (as recommended by Ferrier (2002) and Roberge and Angelstam (2002)), in plans to conserve old-forest ecosystems. The analysis of area-limited focal species allows us to address first the issues of landscape configuration and reserve design not possible with the lesser-studied taxa. Our owl and fisher-specific analysis, however, will use an analytical framework that anticipates, and is compatible with, the subsequent analyses that will integrate data from the other taxa.

Our objectives here are to (1) compare the habitat needs of owls and fisher using a reserve-selection algorithm, (2) explore the ramifications of managing habitat for owls and fishers collectively, (3) compare the areas of predicted high value for fishers and owls with existing reserves, and (4) establish the groundwork to compare the output of the fisher-owl analysis with a similar, subsequent analysis for a taxonomically and functionally disparate set of species.

## 2. Methods

Maps of predicted habitat suitabilities for the northern spotted owl and the fisher originated from published regional-scale habitat models developed by relating broad-scale vegetation and environmental variables to either detections at track plates (fisher; Carroll et al., 1999; Fig. 2) or acoustic survey results (owl; Zabel et al., 2003; Fig. 1). The models estimated the probability of occurrence which, henceforth, we refer to as habitat suitability. Predicted habitat suitability values were assigned to 1 ha (fisher) or 0.16 ha (owl) units within the species-specific study areas. Both exercises included model-building and validation data sets, differing only in the fact that the owl model was selected from among candidate models whereas the fisher model was built using a stepwise variable selection approach.

The owl model (Zabel et al., 2003) was developed by soliciting professional opinion and referencing relevant literature to create and test alternative habitat descriptions that could best predict owl occurrence. Their best model was used to generate a predicted habitat surface that was tested with independent data. The fisher model was developed using the results from pre-existing track-plate survey data and tested using independent survey data collected at systematically arrayed forest inventory (FIA) plot locations (Carroll et al., 1999). The owl model resulted in a habitat suitability map that included four national forests in northwestern California (Six Rivers, Shasta-Trinity, Klamath, and Mendocino National Forests). The fisher model was extrapolated to all lands in the region, but was not projected as far east as was the owl model (see dotted line in Fig. 4). For species comparisons we included only the area where predictions occurred for both species, which included a 20,372 $km^2$ area that comprised the majority of the national forest area in the region (Fig. 4). There are regions, east and west of this common area, where fishers and owls occur and where the original models have predicted suitable habitat. Importantly, the study area that is the focus of this investigation is centered on the current range of both species, even though there is suitable habitat predicted to occur outside this area.

The Forest and Rangeland Renewable Resources Research Act of 1978 authorized and promoted a nationwide survey of renewable resources (Frayer and Furnival, 1999), resulting in the establishment of the FIA program. The design consists of sample points located in a systematic hexagonal grid (centers of each hexagon spaced 5.47 km apart) across all ownerships in the United States, with environmental variables (e.g., characteristics of live and dead vegetation and topography) measured at each point once every 10 years (Roesch and Reams, 1999). FIA data are used to assist in planning and monitoring forest structure and plant communities over large areas (e.g., a Region or a National Forest). Because the fisher model was evaluated using sampling at FIA plots, and because taxa (salamanders, mollusks, lichen, fungi, mosses) that will subsequently be integrated with the owl and fisher

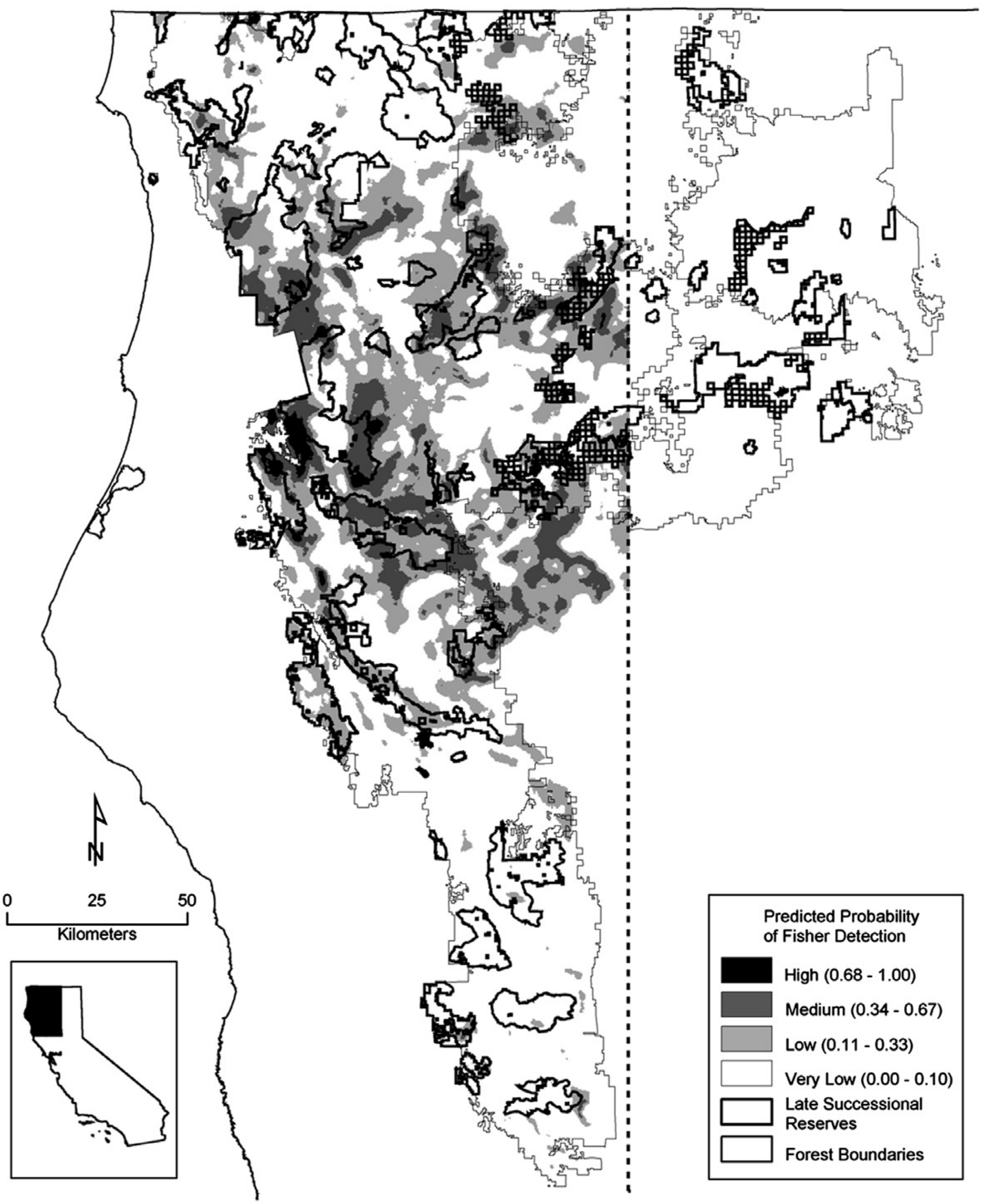


**Fig. 2 – Landscape habitat suitability map for the fisher in northwestern California (Carroll et al., 1999).**

analysis (see Section 1) are sampled only at FIA plots, our modeling framework primarily used the FIA points as reference locations for predicted habitat value. We attributed each FIA point for spotted owl and fisher habitat value based on the mean predicted habitat suitability value from all pixels in a circular landscape around each FIA point with a diameter equal to the mean distance between FIA points (5.4 km). This resulted in predicted values at the 1099 FIA inventory points that fell within the boundaries of the study area (Fig. 4).

### 2.1. *Correlations in predicted habitat suitability*

The predicted habitat suitabilities that resulted from the owl and fisher model are dependent on both the overall abundance of the species and on the effectiveness of the survey method (i.e., the probability of a false negative varies between species). Thus, the average suitability values, calculated using the original grid values, differ greatly between the species (mean [SD] fisher, 0.128 [0.153]; owl, 0.429 [0.283]). Therefore, we used the Spearman rank correlation to evaluate overlap

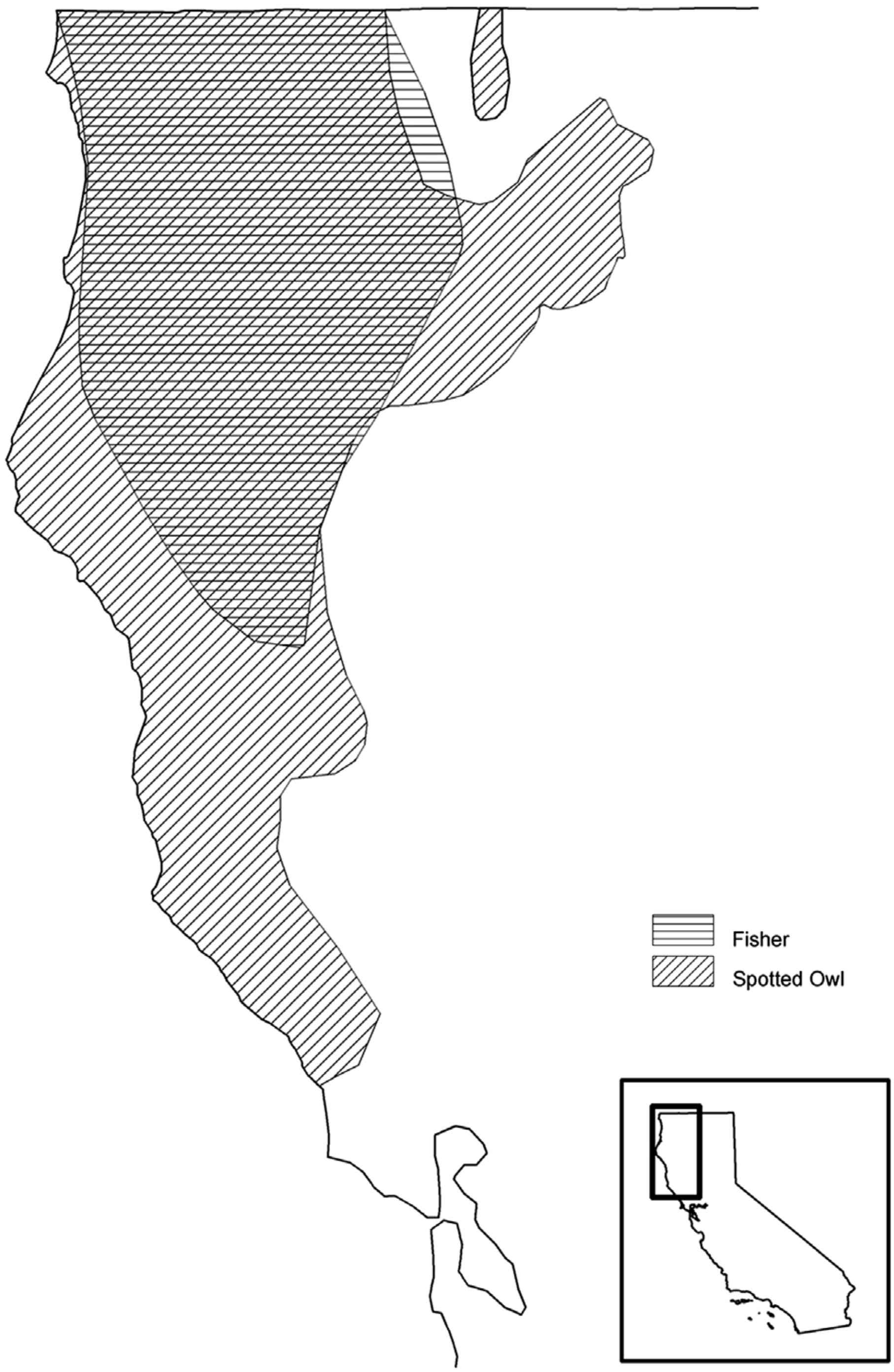


**Fig. 3 – Extent of occurrence of northern spotted owls and fishers in northwestern California, adapted from Zielinski et al. (1995) and Gutiérrez and Barrowclough (2005).**

in predicted habitat value between species. Rank correlations were conducted in two ways: (1) on the original predicted values by resampling (averaging) both the owl grid and the fisher grid to a 100 m (1 ha) resolution, resulting in 2,037,287 cells, and (2) on the value of habitat for each species predicted for the 5.4 km-diameter circle centered on each of the 1099 FIA (inventory) points.

Because both species have been described as associated with old-growth forest conditions, we also compared their predicted suitability values with two measures of forest age and structural development status. The first was the result of a discriminant model that was developed to distinguish between three forest age classes (young, mature, old) in Douglas-fir (*Pseudotsuga menziesii*)/hardwood forests (Bingham and Sawyer, 1991) and which was adapted to FIA inventory plots by Dunk et al. (2004). This model estimated for each inventory plot the probability that it would be included in the old-growth class. The second measure was forest age, the average age of trees on inventory plots that were cored and aged by counting growth rings. Average age correlated

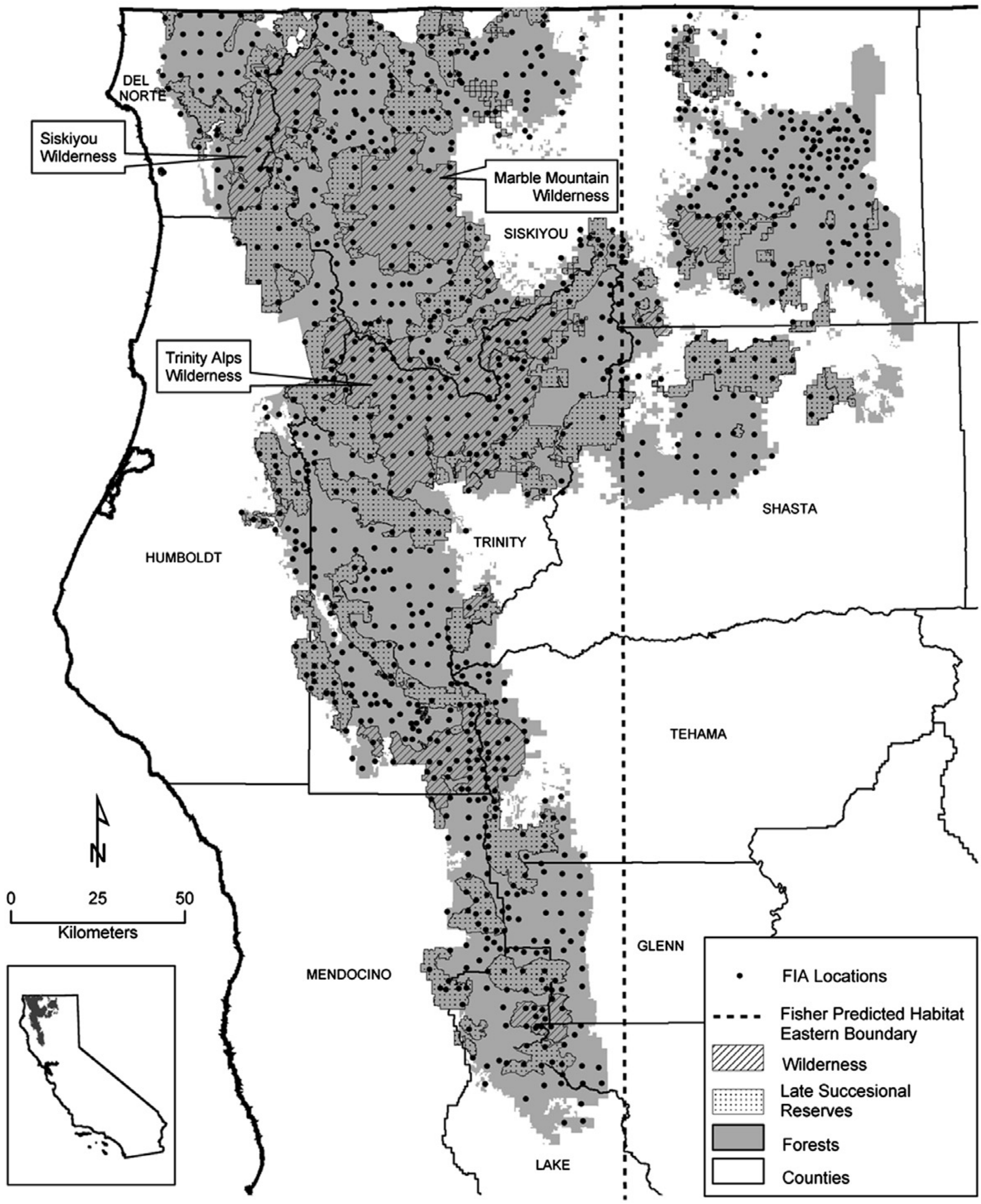


**Fig. 4 – Study area boundaries including portions of Humboldt, Del Norte, Siskiyou, Shasta, and Trinity Counties and portions of the Six Rivers, Klamath, Mendocino and Shasta-Trinity National Forests. Black circles indicate the location of the 1099 Forest Inventory and Analysis (FIA) plot locations, cross-hatched polygons are designated Wilderness, stippled polygons are Late-Successional Reserves, and the gray shaded background represents the area of national forests.**

strongly with maximum cored tree age ($R^2 = 0.72$) and is, therefore, also a good index for the age of the oldest tree on the plot. Spearman rank correlation coefficients compared the suitabilities for each species with each of the two measures of old growth forest condition at each inventory plot, even though the different sized assessment areas (the plot vs. the area for which suitability was assessed around the plot) affect the precision of this comparison.

### 2.2. *The selection of priority areas*

The site selection software, MARXAN (Ball and Possingham, 2000) uses a "simulated annealing" algorithm, a term that is derived from the analogous process of heating and then slowly cooling metals to obtain a strong final structure. This is a Monte Carlo procedure for minimizing multivariate objective functions. Simulations are initialized with a set of planning units drawn at random and then planning units are added to and removed from the set in a series of interactions with the value of each new set compared with that of the previous set until an equilibrium solution is achieved using the smallest number of planning units (Cook and Auster, 2005). MARXAN minimizes the sum of the variables cost, species penalty, and boundary length. Cost is the total monetary or area cost of all planning units selected for the network, species penalty is a cost imposed for failing to meet target goals, and boundary length is a cost determined by the total boundary length of the network (Andelman et al., 1999; Possingham et al., 2000).

We used the inventory points as the basis for planning units. The planning units were created by tessellation (Bailey and Gatrell, 1995) such that the planning surface was divided into a set of 'tiles' (polygons) surrounding the set of inventory points. Each was attributed with a predicted habitat suitability value for each species (see above). The use of predicted habitat suitability values in site selection exercises (e.g. Margules and Nicholls, 1987; Williams and Araújo, 2002), results in a non-zero probability value at each unit in the study area and has advantages over the use of the presence-absence data (Cabeza et al., 2004). These probabilities allow site selection to be recalculated, without the collection of new survey data, when predictors of habitat suitability change. Probabilities of occurrence can also be used as resource selection probability functions (Manly et al., 2002) from which population status and persistence can be estimated (Boyce and MacDonald, 1999; Araújo et al., 2002).

MARXAN performed $10^6$ iterative attempts to find the minimum cost solution per run and performed 100 such runs for each alternative scenario we explored. MARXAN reported the best (lowest cost) solution from each run of $10^6$ iterations, as well as which out of those 100 top candidates had the lowest cost. MARXAN has the option of forcing the inclusion (locking in) of certain areas in the network of priority areas (Ball and Possingham, 2000). We used this option on some occasions to require the inclusion of congressionally designated Wilderness areas or Late-Successional Reserves, or both. The remaining public lands were considered eligible for either inclusion or exclusion. When Wilderness areas are locked in, the program only adds planning units that contain targets whose goals are not met within the current Wilderness system. Locking in protected areas recognizes that, from a practical standpoint, achieving conservation goals within current reserves is easier than adding unprotected areas. We evaluated alternate scenarios that locked in Wilderness areas, Wilderness areas and current Late-Successional Reserves, and no areas. The latter option allows assessment of the distribution of habitat suitability value across the landscape without regard to current management boundaries (i.e., the 'floating site' approach to reserve selection; Williams, 1993). Wilderness and LSR boundaries, for the purposes of implementing MARXAN, were not their explicit boundaries but instead were the boundaries of polygons of inventory points that fell within Wilderness and LSRs.

Goals for each species were expressed as a percent of the total habitat "value" (i.e., predicted probability of occurrence) in the study area. This was considered more realistic than the approach of classifying areas into either a 'suitable' or 'unsuitable' class. A range of goals from 25% to 75% was evaluated. Because almost all areas have a non-zero habitat suitability value, the entire region would be needed to achieve a goal of 100%. When the goal is to achieve a target habitat value for both species, MARXAN computes shortfalls for each species separately until areas that meet the target value are included.

MARXAN requires an estimate of the cost of including each new site in the conservation network. Neither monetary or opportunity cost data were available for public lands in this region so we assumed that each FIA point (which are spaced on a regular grid) had equal cost. The Boundary Length Modifier is most useful to minimize the fragmentation of priority areas when the reserve is designed for many species whose occurrences are distributed among widely disjunct planning units. This is not the case for this analysis, which is focused on two species whose forest habitat is already relatively contiguous in the study area. We did not use the Boundary Length Modifier because preliminary results, where the modifier was included, produced very similar results. The Species Penalty is used in MARXAN primarily when a large number of species are to be included and lower Species Penalty values allow more approximate solutions to target values. However, when MARXAN is used to select priority areas for only 1 or 2 species, such as our situation, Species Penalty values must be set high enough (we used 10) to guarantee that the outcome never fell short of the target goal. MARXAN evaluated scenarios based largely on the relationship between the amount of habitat value captured and the total number of planning units reserved.

## 3. Results

### 3.1. *Correlations: suitability values*

The rank correlation between habitat values for the spotted owl and the fisher, using the habitat suitability values at normalized 1 ha grid cells, was 0.111. This value increased to 0.162 when the suitabilities were compared using the suitability value for the circular area around each inventory point (Table 2). The areas of highest predicted suitability overlap were in the central portion of the study area because predicted fisher habitat suitability decreased to the north and south of this area, whereas predicted owl suitability did not (Fig. 5). Spotted owl habitat had a slightly stronger rank correlation with tree age and the Bingham and Sawyer (1991) 'old-growth condition', 0.257 and 0.258, respectively, than did fisher (0.198 and 0.240, respectively). Correlations with predicted probability of old-growth condition were slightly higher, regardless of species, than correlations with mean tree age (Table 2).

### 3.2. *Scenarios with goals expressed as a percent of total habitat*

#### 3.2.1. *Spotted owl and fisher scenarios compared*

To capture 25%, 50% and 75% of the total habitat value for the spotted owl required 14.0%, 29.2%, and 47.3% of the inventory points, respectively, whereas capturing the same percentages of habitat value for the fisher required only 5.3%, 13.5%, and 27.2% of the inventory points, respectively (Fig. 6a). When the Wilderness areas were 'locked in' the priority areas that

**Table 2 – Spearman rank correlation coefficients for the relationship between spotted owl and fisher predicted habitat suitabilities (at the resolution of 2,037,287 1-ha grid cells (grid) and for the average in a 5.4 km-radius circle assigned to each of the 1099 FIA inventory point (inventory point)), and for the relationships between each species and estimated probability of old-growth status and mean tree age at FIA plots**

| | Fisher (grid) | Fisher (inventory point) | Predicted old growth | Tree age |
|---|---|---|---|---|
| Spotted owl | 0.111 | 0.162 | 0.258 | 0.257 |
| Fisher | – | – | 0.240 | 0.198 |

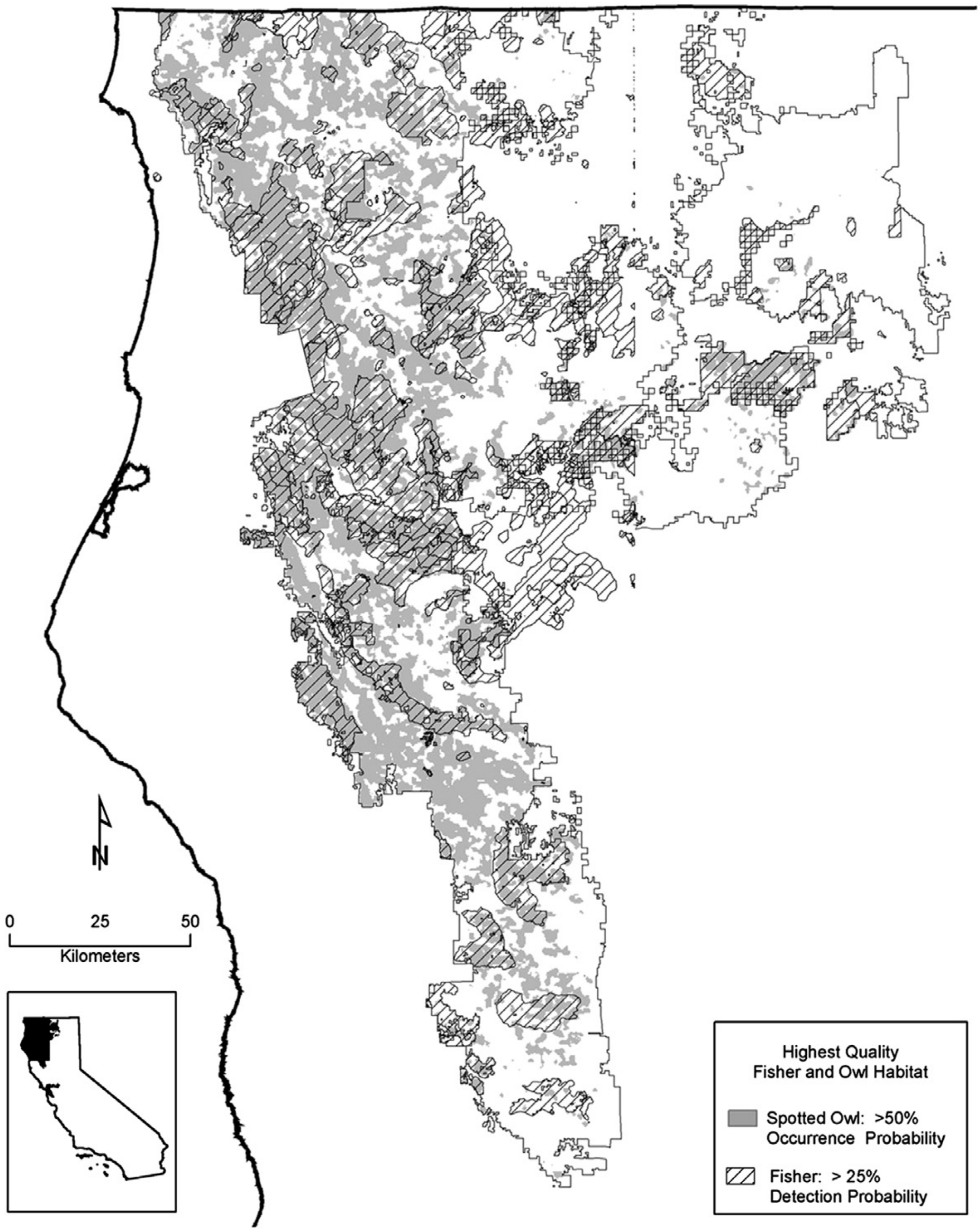


**Fig. 5 – Highest predicted fisher habitat suitability (crosshatched polygons: >25% detection probability; Carroll et al., 1999) overlaid on the highest predicted owl habitat suitability (gray background: over 50% occurrence probability; Zabel et al., 2003).**

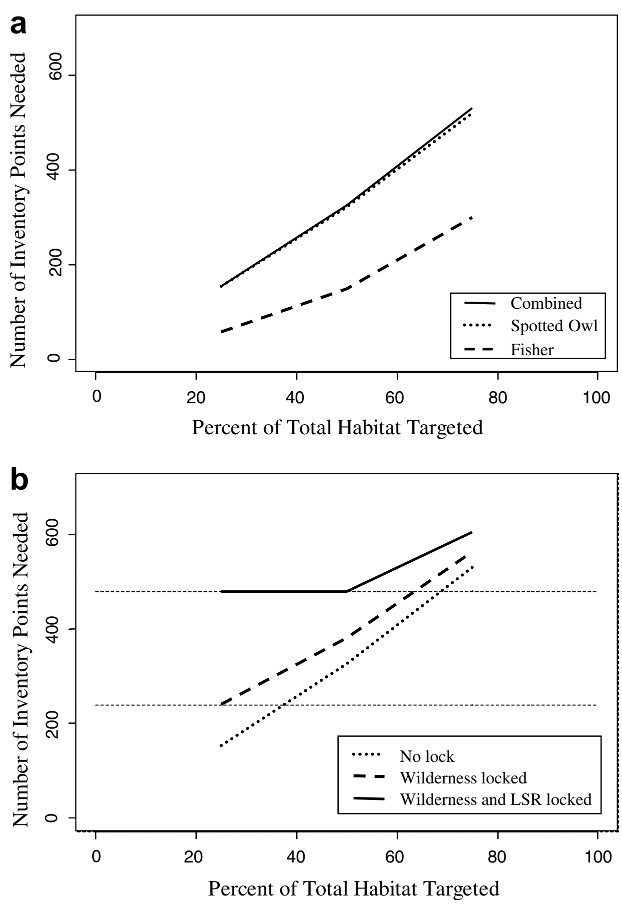


**Fig. 6 – Results of MARXAN site-selection relating the number of inventory points needed to capture increasing percentages of total habitat value for: (a) spotted owls, fishers, and owl + fisher combined, and (b) the owl + fisher combined scenario, when increasing amount of area in reserve is locked-in.**

were added for the spotted owl were more widely distributed, on both the north-south and the east-west axes, than for the fisher (Fig. 7a and b).

3.2.2. *Combined owl-fisher scenario*

Capturing 25%, 50% and 75% of habitat value for both the owl and the fisher requires 14.0%, 29.7%, and 48.3% of the inventory points, respectively (Fig. 6a). Ignoring current protected areas, the priority area that optimized fisher *and* owl habitat goals was aggregated in the western portion of the study area and was distributed more broadly from north to south than for the fisher alone (Fig. 8). Starting with the existing Wilderness reserve system locked in (which alone comprised 21.7% of inventory points), capturing 25%, 50%, and 75% of the habitat value required 21.8%, 34.7%, and 51.3% of the inventory points, respectively (Fig. 6b). Starting with both the Wilderness *and* the Late-Successional Reserves locked in (obligating 43.6% of the inventory points) increased these requirements to 43.6%, 43.6%, and 55.0%, respectively. The identical values for 25% and 50% are due to the fact that Wilderness and Late-Successional Reserves already capture more than 50% of total habitat value for each species, so no new sites need to be added to achieve either target value.

Forcing the inclusion of existing reserves in the optimal owl-fisher network requires a greater number of sites because the network must include suboptimal areas that occur in existing reserves. When Wilderness and Late-Successional Reserves are locked into the system, capturing 75% of the combined habitat value requires areas that connect protected areas and that are also well distributed in the study area (Fig. 9).

### 3.3. *Scenarios with goals expressed as a fixed area*

3.3.1. *Spotted owl and fisher scenarios compared*

In these scenarios, MARXAN was parameterized to find an area *equivalent in size* to the current area of the Late-Successional Reserve system (5824 $km^2$, or 240 of 1099 inventory points) that could, in combination with current Wilderness areas (locked into this scenario), optimize habitat representation for each species. This is different than locking-in the explicit locations of the Late-Successional Reserves. Instead, here we assume the Late-Successional Reserves do not exist and we ask how different this network would appear if it occupied the *same total area* as the current system, but was created based solely on predicted species habitat suitability values. For the spotted owl, priority areas under this scenario were more aggregated than the current Late-Successional Reserve system (Fig. 10a) but were more fragmented than when the selection process was constrained only by habitat value thresholds. The percent overlap, in terms of number of inventory points, between the current reserves (Wilderness and Late-Successional Reserves combined) and the network of new priority areas selected by MARXAN for the spotted owl was 72.6%. This number dropped to 45.2% overlap when the Wilderness areas were excluded from the comparison (Table 3).

For the fisher, new priority selected areas overlapped less with Late-Successional Reserves (Fig. 10b) than for the owl. This occurs primarily because the Late-Successional Reserves are fairly evenly distributed within the study area but habitat value for the fisher is more aggregated than for the owl. Additions that optimized representation of fisher habitat were uncommon on the Mendocino National Forest or the northern Six Rivers National Forest, and instead favored areas on the eastern portion of the Klamath National Forest (Fig. 10b). The additions largely connected the existing Wilderness areas (identified in Fig. 4) by including the lower elevation regions between them. The percent overlap between the current protected areas (Wilderness and Late-Successional Reserves combined) and the new network of priority areas selected by MARXAN for fishers was 69.7%. This dropped to 39.4% overlap between the MARXAN-selected areas and the Late-Successional Reserves only (Table 3), suggesting a relatively poor spatial association of areas of high predicted fisher habitat value and the current Late-Successional Reserve system.

3.3.2. *Combined owl-fisher scenario*

Optimizing representation of both owl and fisher habitat, under the 'fixed area' constraint resulted in priority areas that were located at low to mid-elevations in eastern Humboldt, western Siskiyou, and northern Trinity Counties on the Six Rivers and Shasta-Trinity National Forests (Fig. 10C; counties

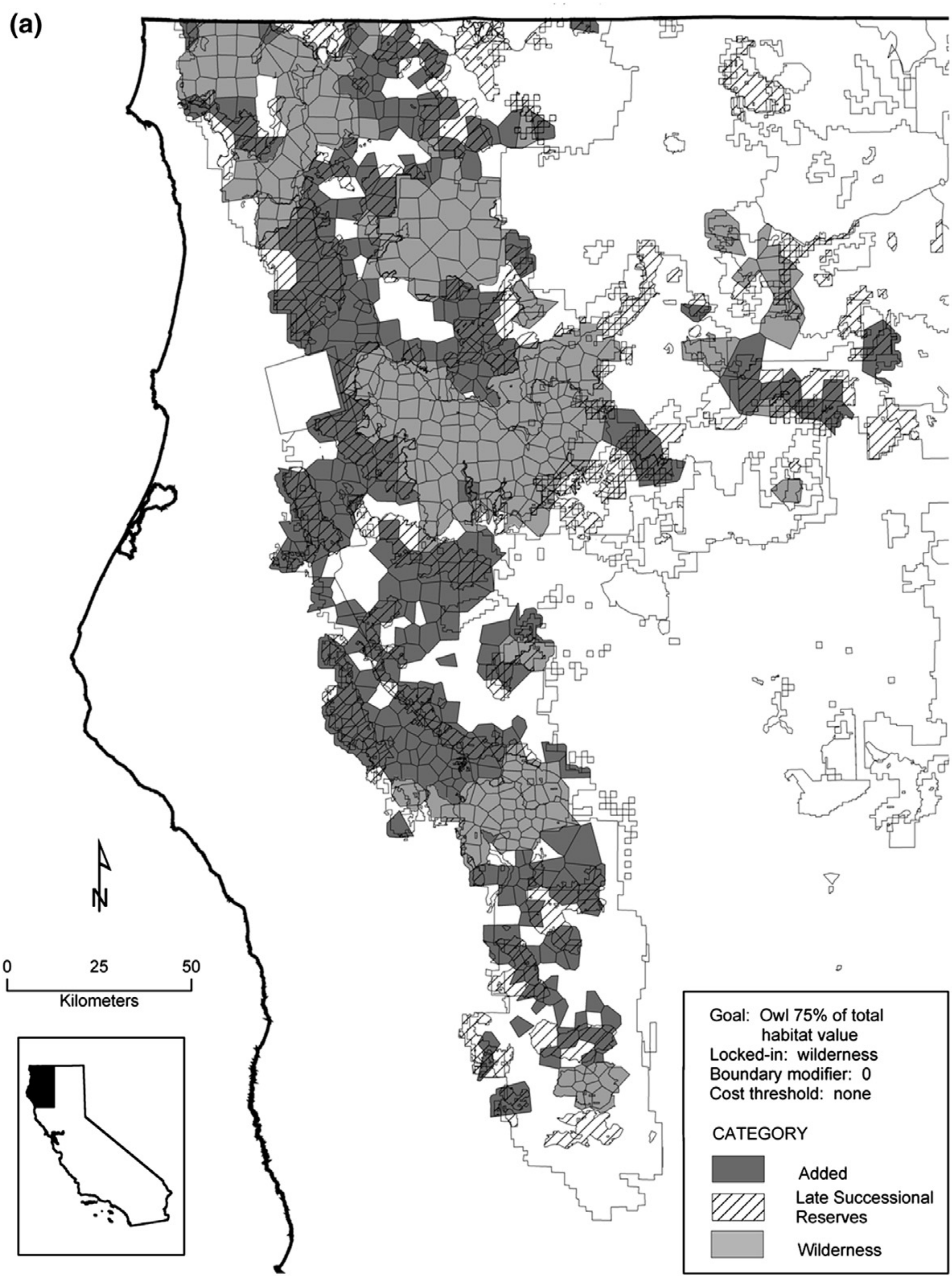


**Fig. 7 – Map of priority areas (in black) for the *spotted owl* (a) and *fisher* (b) when the target is 75% of total habitat value. Polygons represent tessellation tiles centered on the inventory point locations. Wilderness areas (gray polygons) were locked in.**

identified in Fig. 4). This scenario resulted in a relatively compact array of additions that was centered in the central and northwestern portion of the study area. It appeared to be influenced strongly by the clumped distribution of fisher habitat suitability value, in that the combined scenario resembled the fisher scenario more closely than it did the more dispersed owl scenario (compare Fig. 10a and b). This network, which was optimized to select the best combination of owl

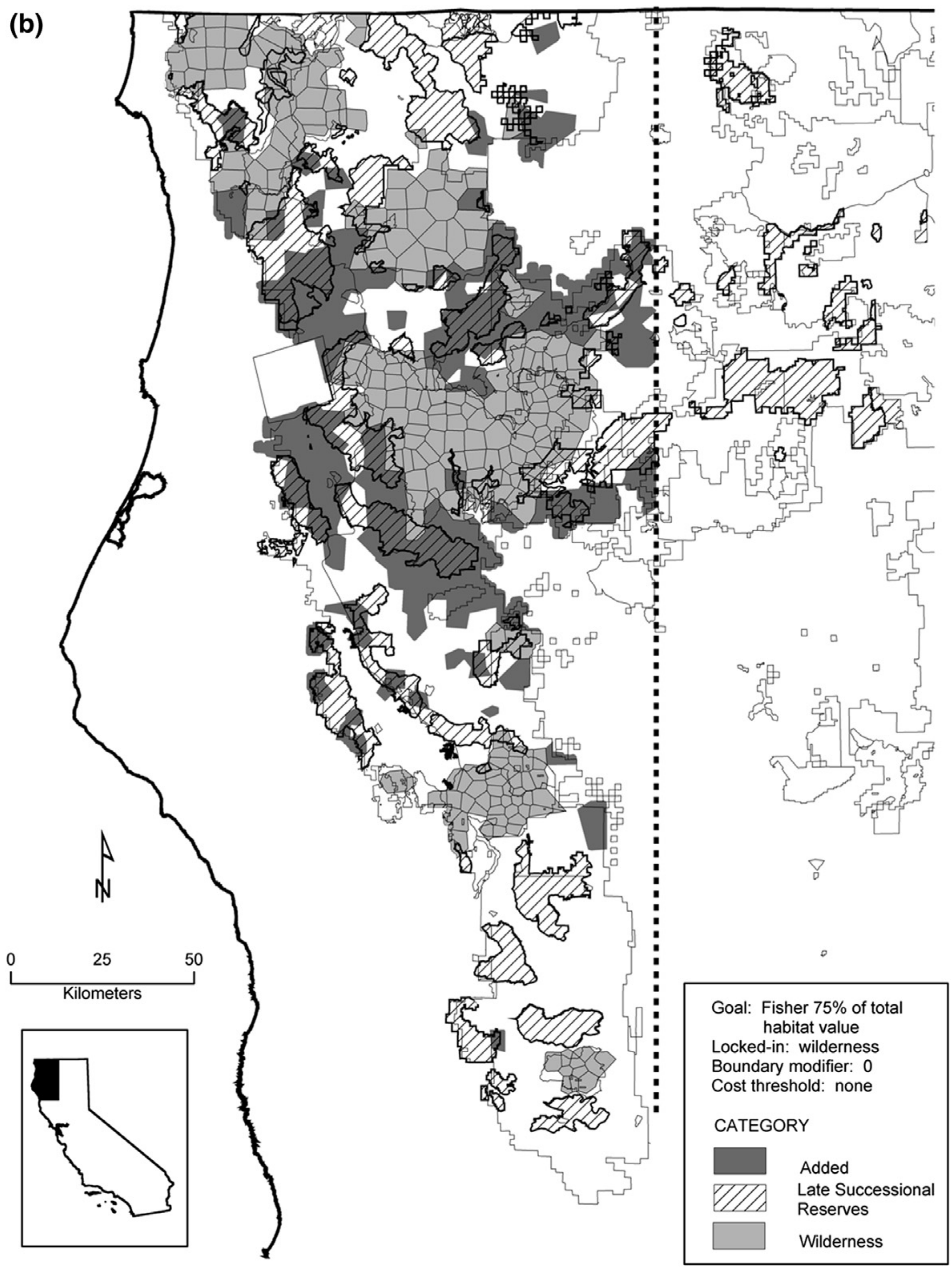


**Fig. 7 – *continued***

and fisher habitat value – and that was equivalent in area to the total of the current Wilderness and Late-Successional Reserve system – captured 71.6% of their total habitat value (Table 4), compared to the 55.3% captured by the current locations of Wilderness and Late-Successional Reserves combined. Networks optimized for either the owl or the fisher alone were intermediate in mean percent of combined habitat value captured (Table 4). The percent overlap, in terms of number of inventory points, between all reserves (Wilderness and Late-Successional Reserves combined) and the new net-

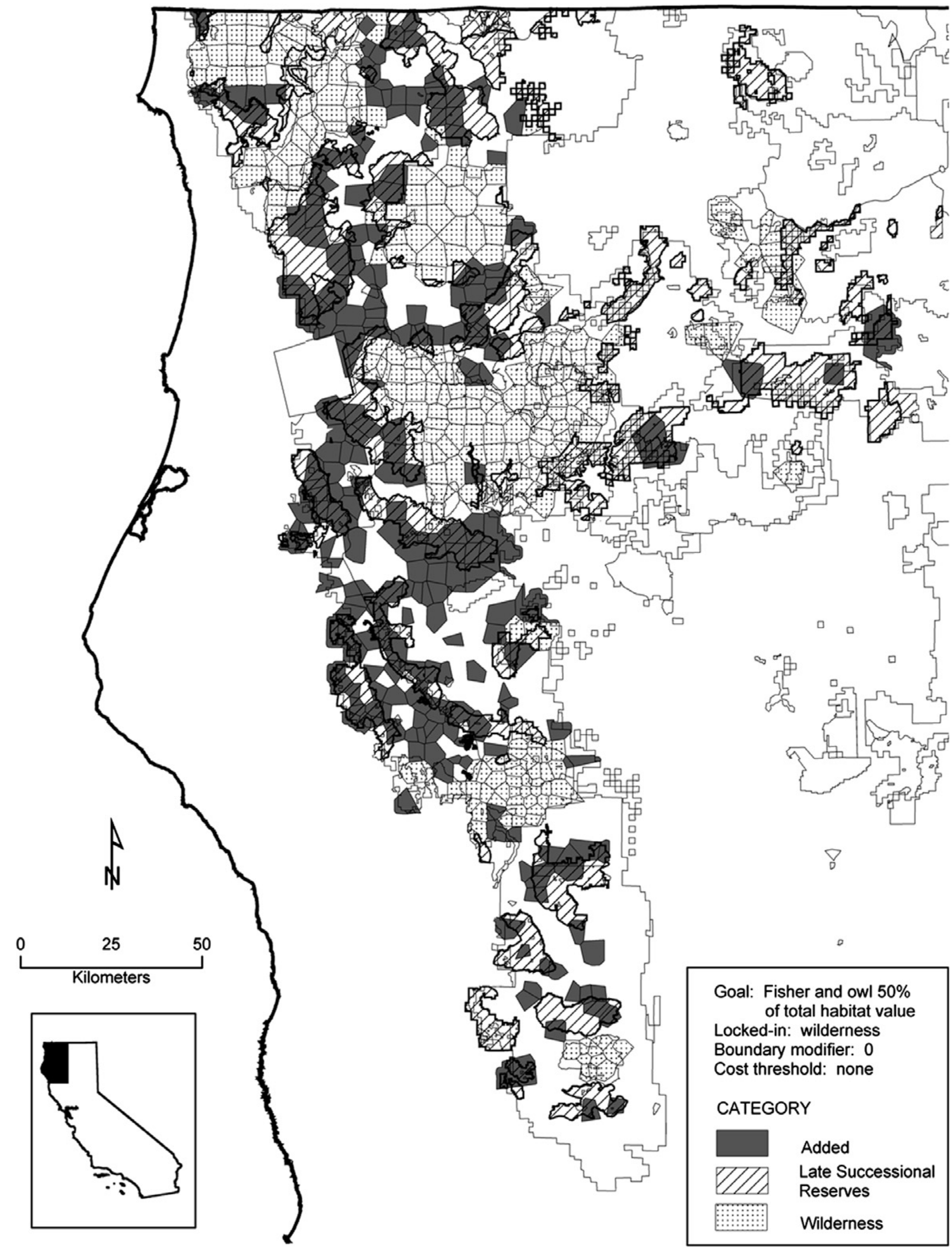


**Fig. 8 – Priority areas for *spotted owl and fisher combined* (black) with a target of 50% of total habitat value. Wilderness areas (stippled) were locked in.**

work of priority areas selected by MARXAN, for the spotted owl and fisher combined, was 70.4%. This number dropped to 40.7% when Wilderness areas were excluded from the comparison (Table 3).

## 4. Discussion

Setting conservation goals (e.g., amount of habitat) in a site selection algorithm is often difficult because information is

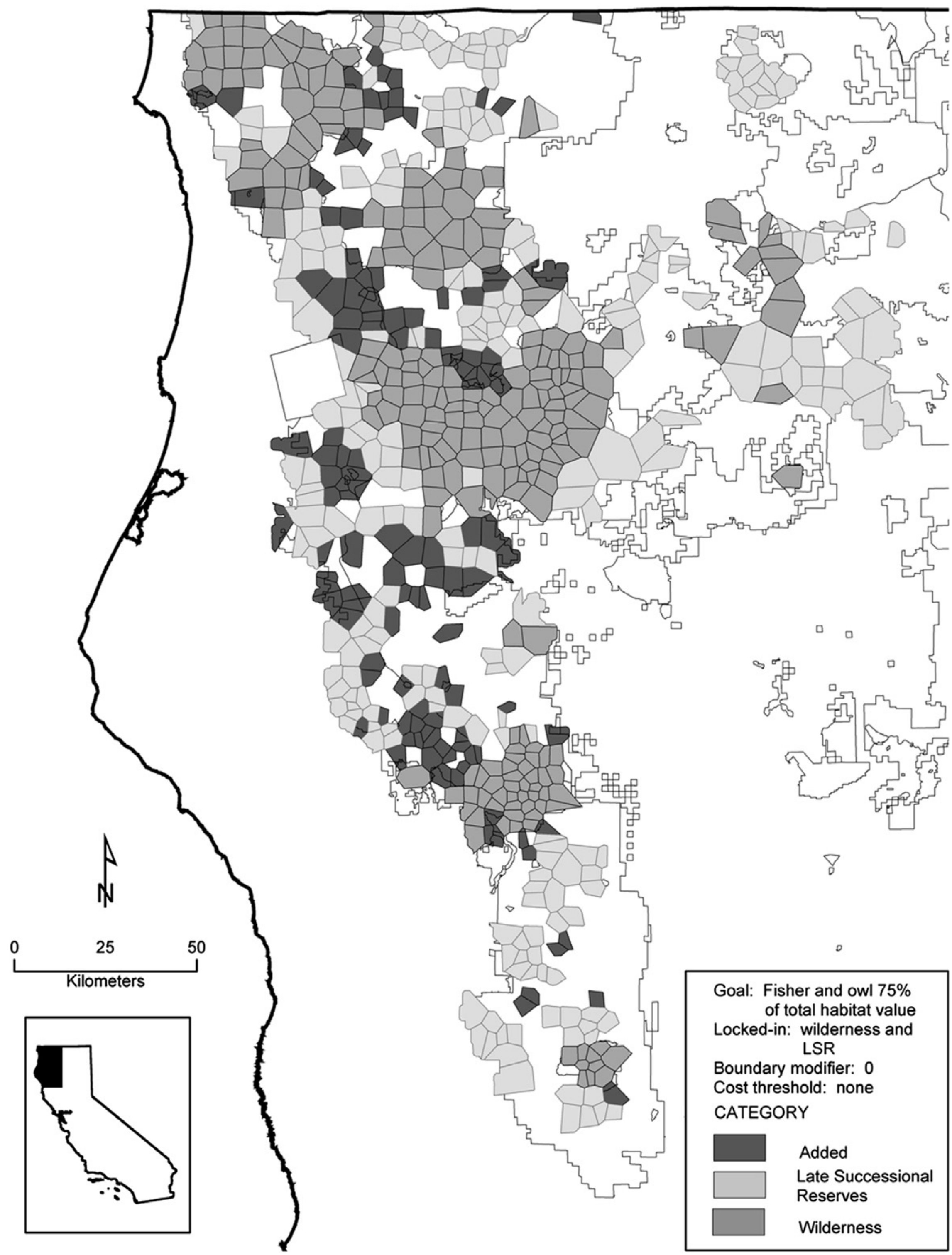


**Fig. 9 – Priority areas for *spotted owl and fisher combined* (black) with a target of 75% of total habitat value with Wilderness (dark gray) and Late-Successional Reserves (light gray) locked in.**

unavailable on the threshold amount of habitat necessary to insure population viability. Our analysis does not directly address the question of "how much is enough?" but evaluated the overlap in priority areas between fishers and spotted owls over a range of habitat goals. The association of the spotted owl and the fisher with elements of late-successional conifer-dominated forests is well established (Forsman et al., 1984; Solis and Gutiérrez, 1990; Carey et al., 1992; Powell and Zielinski, 1994; Franklin et al., 2000; Zabel et al., 2003; Zielinski et al., 2004b). On this basis, the selective use by these species of large standing live and dead trees, and dense cover appear similar. Our analysis supports the association of both species

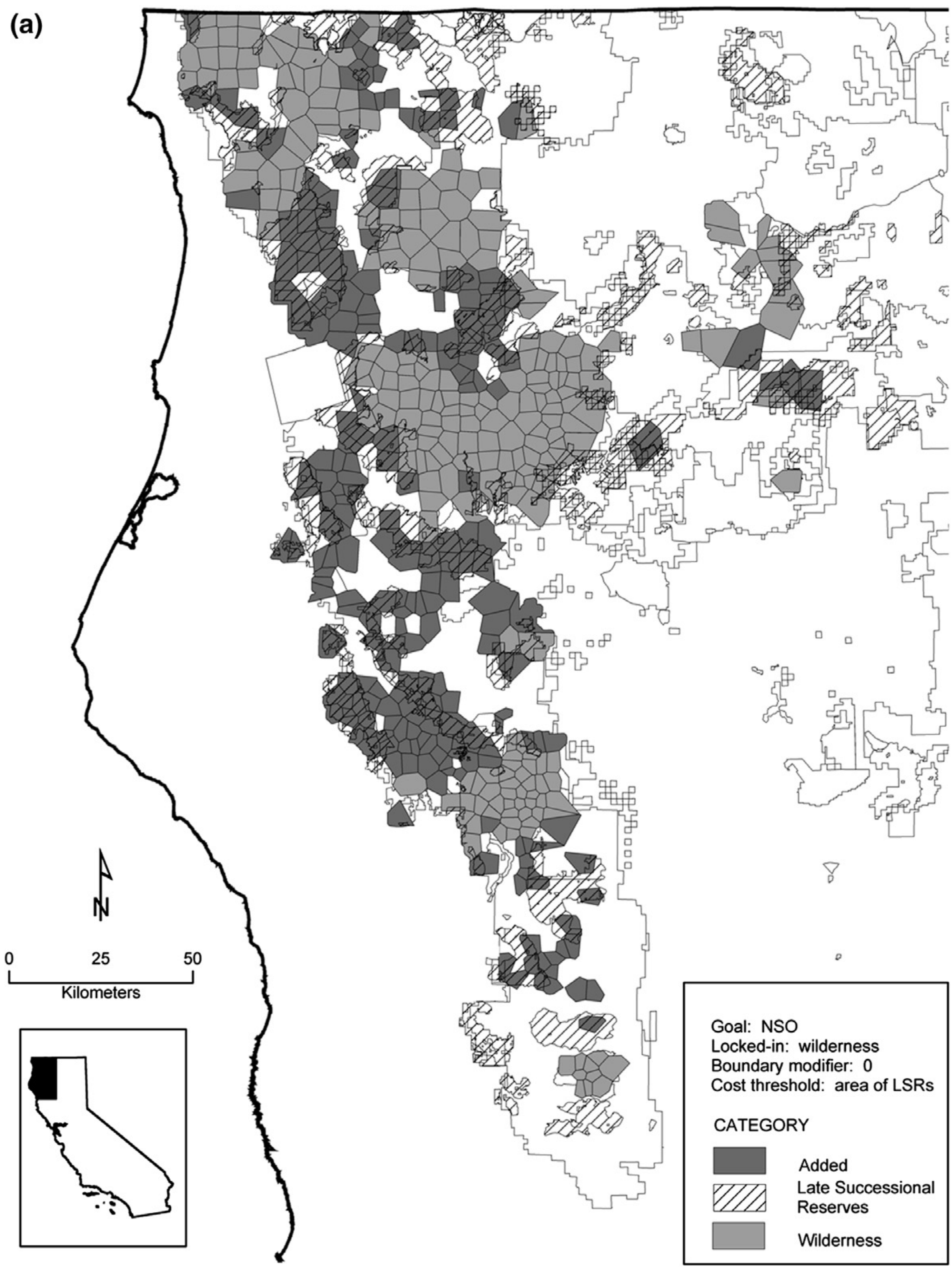


**Fig. 10 – Priority areas (black) for the *spotted owl* (a), *fisher* (b) and *spotted owl and fisher combined* (c) that are equivalent in area to the combined area of Wilderness (gray) and Late-Successional Reserves (cross-hatched). Wilderness areas were locked in.**

with old-forest attributes because both have similar strength of relationships with estimates of forest age and of old-growth status at the inventory plots. The fisher's correlation with tree age was a bit weaker than that for the owl, which may be because the best fisher habitat is more concentrated in the lower-elevation biologically productive zones in the western portion of the study area, where stands can achieve complex habitat structure when trees are relatively young.

Our analysis extends the question of similarity of habitat from the use of similar habitat *elements and stands*, to ask whether the areas of predicted *landscape habitat suitability* are also similar. And, if they are, how coincident are the

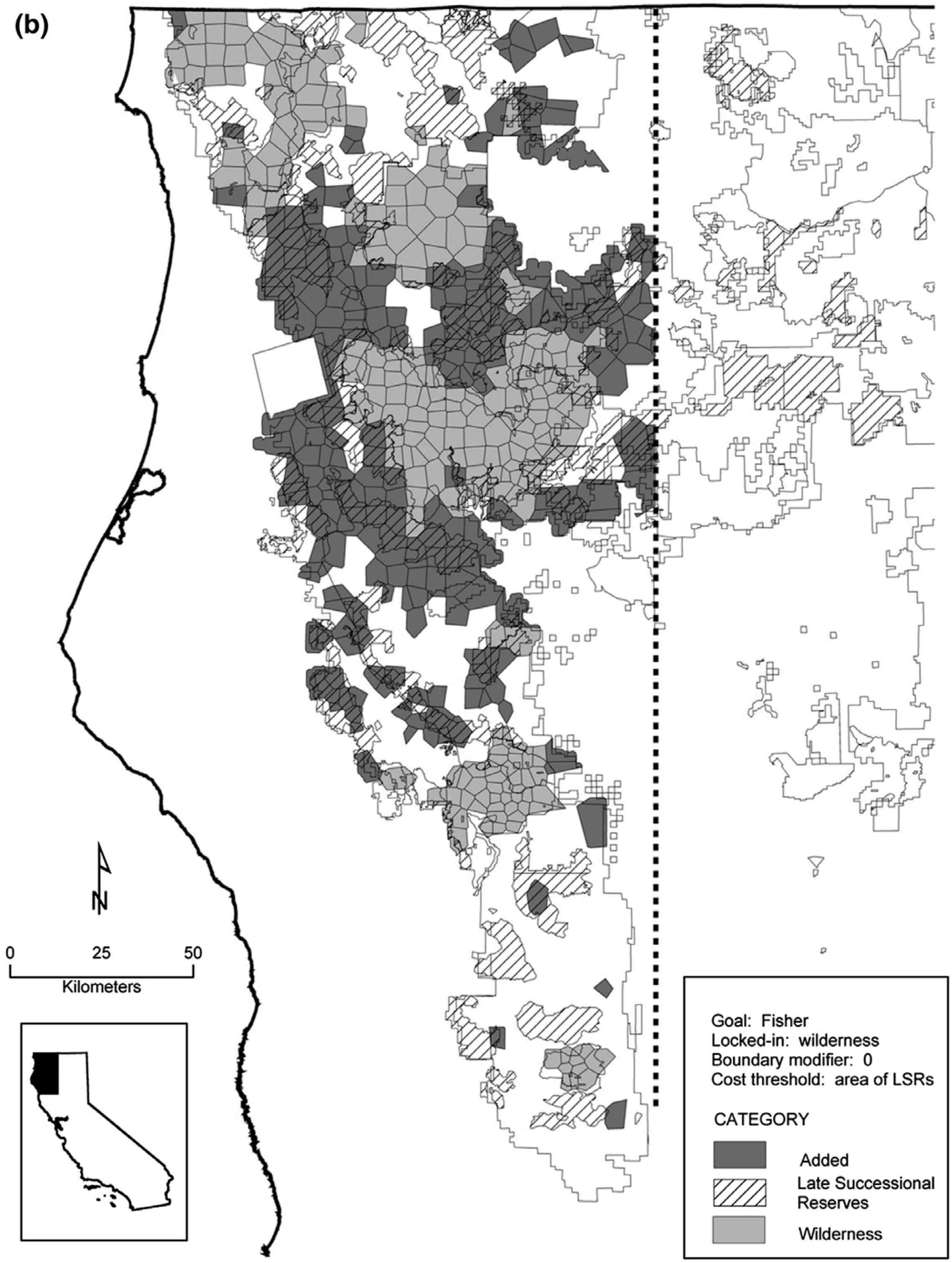


**Fig. 10 – *continued***

areas of high suitability for each species with reserves that have been established for biodiversity protection? This is of special interest for the spotted owl because the Late Successional Reserves were established with spotted owl conservation as a goal. If areas of high predicted suitability occur in the same areas for both species, this would support the hypothesis that owls and fishers share more than the use of specific habitat elements; their populations also have a similar response to the environmental variation that occurs across ~26,000 km$^2$ of land in northwestern California. Support for this hypothesis would greatly simplify the management of forest lands for these two species of conservation

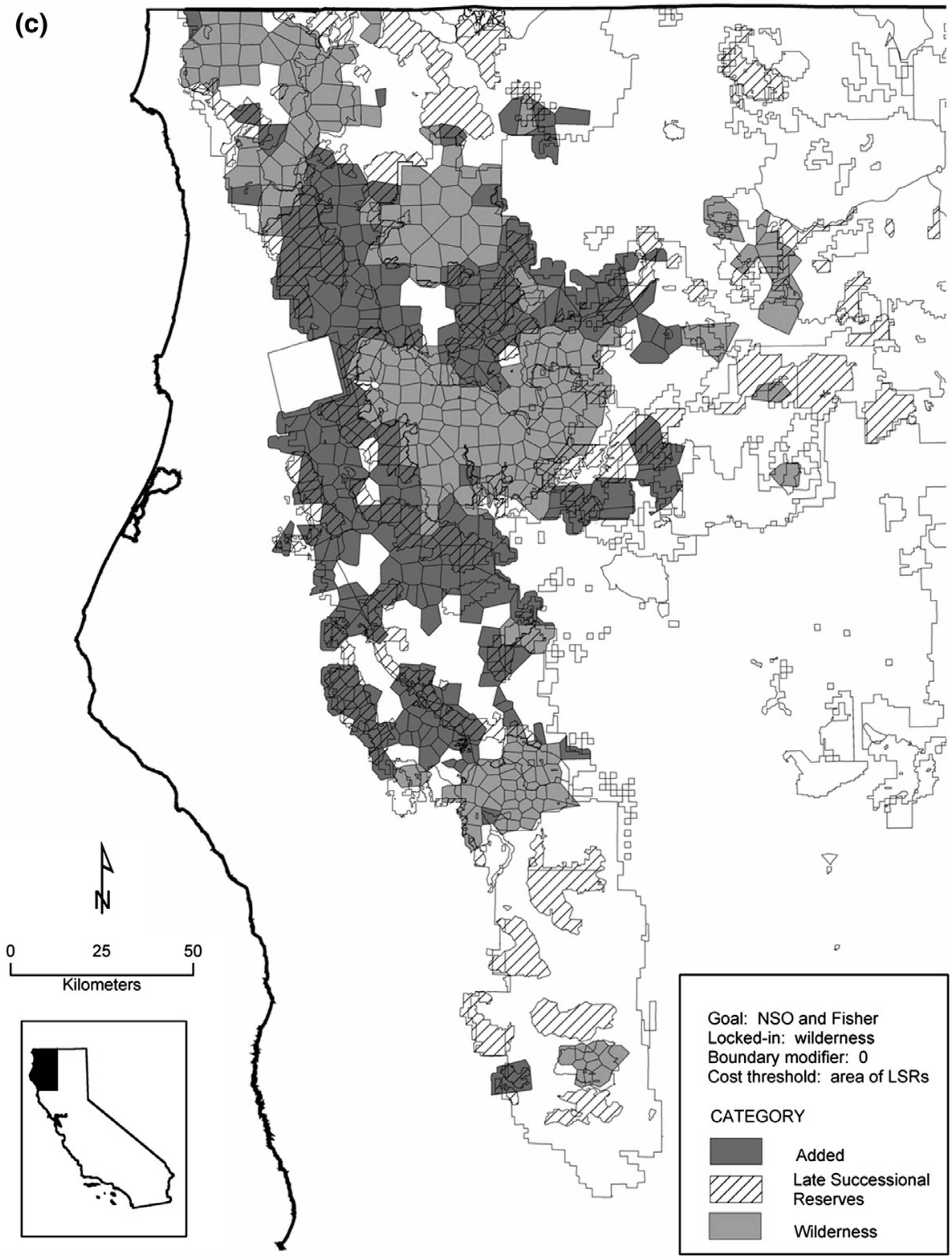


**Fig. 10 – *continued***

concern. In the most strict, quantitative sense, the correlation data do not strongly support the hypothesis. On either a pixel-by-pixel basis, or on the basis of predicted value immediately surrounding each forest inventory point, the correlation between the relative ranked habitat value of owls and fishers was not strong ($r < 0.20$). The correlation analysis suggests that fishers and owls differ in their response to the habitat features distributed within landscapes, or that they have distributed their populations differently within the study area.

One reason for the poor correlation may be because the highest ranked habitat for fishers is more localized in the

**Table 3 – The percent overlap in the MARXAN-selected priority area solution and pre-existing reserves (Wildernesses and Late-Successional Reserves) when fisher only, spotted owl only, and spotted owl + fisher combined are considered**

| | Species or combination | | |
|---|---|---|---|
| | Fisher | Spotted owl | Fisher + Spotted owl |
| Overlap between the MARXAN priority area solution and existing reserves (Late-Successional Reserves + Wilderness combined) | 69.7 | 72.6 | 70.4 |
| Overlap between MARXAN priority area solution and Late-Successional Reserves when Wilderness areas are excluded | 39.4 | 45.2 | 40.7 |

Overlap is the percent of inventory points in common, not area shared.

**Table 4 – The average percent of habitat value captured for the fisher, spotted owl and fisher + spotted owl (row headings) when MARXAN created optimal site selection scenarios for each species, and the combination, and for the current Late-Successional Reserve (LSR) system (column headings)**

| | Scenario | | | |
|---|---|---|---|---|
| | Fisher | Spotted owl | Fisher + Spotted owl | LSR |
| Fisher | 82.7 | 57.1 | 82.1 | 54.3 |
| Spotted owl | 55.5 | 65.9 | 61.1 | 56.0 |
| Fisher + Spotted owl | 69.1 | 61.5 | 71.6 | 55.3 |

Wilderness areas were 'locked-in' and the total area was equal to the combined area of current Wilderness and Late-Successional Reserves.

west-central portion of the study area than is habitat for the owl (Fig. 7a and b). Predicted fisher habitat is a decreasing function of precipitation (which varies in an east-west gradient) and a quadratic function of UTM northing (Carroll et al., 1999), a pattern that is not demonstrated for owl habitat (Zabel et al., 2003). This may be due to: (1) different vagilities, and therefore different metapopulation structures of the owl and fisher, (2) other differences in life histories or ecology, (3) stochastic factors that affect patch occupancy, (4) effects of historical factors such as disease or commercial harvest, or (5) subtle differences in the habitat modeling approaches. Regardless of the reason, the difference in spatial arrangement of predicted high-value habitat between species predisposed a relatively poor correlation between ranked habitat values.

The greater contagion of predicted habitat value for the fisher than the owl also influenced the selection of priority areas. The system of priority areas selected for the owl was more dispersed than for the fisher. Capturing the same proportion of total habitat value for the owl required more inventory points (and therefore more area) than for the fisher. Priority areas shared by the owl and the fisher were centered near the western border of Humboldt County with Trinity and Siskiyou Counties, surrounding the Trinity Alps Wilderness and south and west of the Marble Mountain Wilderness (see Fig. 4 for place names). For each species, the areas selected to be added were primarily low-elevation forests located between established higher-elevation Wilderness areas. Previous work on both species supports the finding that high-elevation areas have low suitability, primarily because they lack continuous forest cover, especially the productive mixed hardwood-conifer stands (Aubry and Houston, 1992; Zielinski et al., 1997; Zabel et al., 2003).

The more dispersed nature of the predicted high-value areas for the owl meant that the priority areas for both species combined resembled the areas selected for the owl alone. Thus, the number of inventory points necessary to capture a selected proportion of *combined* habitat value was only slightly greater than for the owl alone (Fig. 6a). Locking-in the Wilderness areas substantially *increased* the amount of area necessary to achieve a selected proportion of total habitat value for both species combined (Fig. 6b). This occurred because the high elevation Wilderness areas, which are suboptimal in habitat value, comprised almost a quarter of inventory points. Forcing their inclusion required more area *outside* Wildernesses to be selected to achieve the habitat value goals. Locking-in the Wilderness areas *and* the Late-Successional Reserves constrained the process even further because this handicapped MARXAN by the forced inclusion of almost half the study area, regardless of its habitat value.

The extent of complete overlap between predicted owl and fisher habitat in northwestern California cannot be directly addressed because the owl habitat suitability model was not applied to non-federal lands. Much of the best fisher habitat in northwestern California appears to be on non-federal lands (Carroll et al., 1999), probably because of regional gradients in geoclimatic factors and vegetation type rather than seral stage, because private lands have much less old forest compared to federal lands (Wadell and Bassett, 1996, 1997). Although owl and fisher habitat are moderately correlated on federal lands, we cannot assume that federal lands can play the same relative role (i.e., contribution to overall population viability) for the fisher as they have been expected to do for the owl (USDA Forest Service and USDI Bureau of Land Management, 1994). Thus, we should not assume that fisher viability in northern California is insured by protections for the spotted owl included in Northwest Forest Plan.

When we developed scenarios that limited the total size of selected areas to an area equivalent to the combined area of the current Late-Successional Reserves, the new network of priority areas for each species were located at substantially different locations than were the existing reserves. We locked-in the Wilderness areas in this scenario because, unlike the Late-Successional Reserves, they are congressionally designated areas that are unlikely to change on the basis of new scientific information, such as that presented here. The priority areas for owls and fishers were more aggregated than the current system of Late-Successional Reserves and the new priority areas never overlapped the existing reserves (Wilderness and Late-Successional Reserves) by more than 73%. Excluding the designated Wilderness from this analysis resulted in overlap proportions closer to 40%, largely because the system of Late-Successional Reserves is more evenly dispersed across the study area than the aggregated areas of high-value habitat, especially for the fisher. Viewed another way, the Late-Successional Reserves captured, on average, only about 55% of the predicted habitat value in the study area for the owl, the fisher, or both species combined. However, the priority areas identified by MARXAN and constrained to include no more total area than the existing Late-Successional Reserves, captured much higher values (61.1%, 82.1% and 71.6% for the owl, fisher, and owl and fisher combined, respectively). Thus, the Late-Successional Reserves capture, on average, 10% and 28% *less* predicted habitat value for the owl and the fisher, respectively, when compared to the new priority areas selected for each species using the empirical habitat models. Importantly, however, the LSRs capture a greater percent of habitat value than do the designated Wilderness areas alone.

The difference in outcomes between the habitat value of existing reserves and habitat model-based priority areas is especially clear when MARXAN was not encumbered by locking-in the reserves. When completely unconstrained, selected priority areas were well-distributed (especially along the north-south axis of the study area) in connected, but smaller blocks (Fig. 8) than the larger contiguous areas that were selected around the existing Wilderness areas when all the reserves were locked-in. When existing reserves could be ignored, the optimal selection of priority areas was based exclusively on the habitat value of the candidate locations and the new system was poorly aligned with existing Late-Successional Reserves.

Although the system of Late-Successional Reserves was influenced by the needs of the spotted owl, Late-Successional Reserves were not established exclusively for the owl; they were the application of conservation biological theory that called for a system of well-distributed reserves for spotted owls (Thomas et al., 1990; Murphy and Noon, 1992) and other late-successional associated species. Thus, it may not be surprising that they are not as efficient at capturing the combined value of owl and fisher habitat as are our species-specific scenarios. Nonetheless, the Late-Successional Reserves, with their emphasis on geographic distribution may lack the connectivity necessary for wide-ranging and non-volant mammals, such as the fisher, compared with the spotted owl.

The Northwest Forest Plan made use of extensive theoretical and simulation studies on the metapopulation dynamics and minimum reserve size and spacing requirements of the spotted owl (e.g., Lande, 1987; Lamberson et al., 1992). Given the influence of the northern spotted owl on the development of the reserve system it was somewhat surprising, therefore, that the existing reserves have only about 45% overlap with the highest value spotted owl areas (as identified in our analyses), and that the existing reserves account for only about 56% of the total regional habitat value for spotted owls. The disparity between the locations of the Late-Successional Reserves and the analysis of the Zabel et al. (2003) model presented here may be due, in part, to the fact that Late-Successional Reserves were designated based on their *potential* to provide mature forest habitats; some are not currently in mature forest condition. Alternatively, the mismatch may be due to the lack of knowledge of the distribution of spotted owl habitat in 1990 and the fact that Late-Successional Reserves were designated at the level of individual national forests, rather than coordinated throughout the owl's range in northwestern California. Alternatively, the disparity may also reflect the fact that spotted owls in northern California are not exclusively associated with late-successional forests (Thome et al., 1999; Franklin et al., 2000; Zabel et al., 2003), which would yield a mismatch between where owl habitat is predicted and where late-successional forests are located. Our results suggest that the Northwest Forest Plan's system of Late-Successional Reserves may not achieve the goal of capturing the best habitat for the northern spotted owl in our study area. The implications of this conclusion should be addressed further by comparing owl vital rates in the priority areas our analysis identified and the Late-Successional Reserves. The current Late-Successional Reserve system does, however, capture a larger percent of total habitat value for the spotted owl than for the fisher, as we originally predicted.

We do not know what proportion of total predicted habitat value need be protected to maintain a viable population because we do not know the relationship between predicted suitability and population size or vital rates. Furthermore, we have not included a mechanism for forecasting change (human and natural disturbances) in the study area and predicting these effects on habitat value and site selection. Resource Selection Functions provide an opportunity to do so (Boyce and MacDonald, 1999), as do spatially explicit population models that assume relationships between habitat value and vital rates (e.g., Schumaker, 1998; Carroll et al., 2003). However, we do know that identifying and connecting areas of current habitat value is better than isolating them and, thus, the scenarios identified by MARXAN probably contribute more to viability than existing isolated Wilderness areas and Late-Successional Reserves.

The most likely explanation for why the system of Late-Successional Reserves does not overlap the best owl and fisher habitat is because the reserves were deliberately dispersed. This occurred to: (1) minimize the risks of catastrophic events (e.g., stand-replacing fire) that could extinguish a few large contiguous reserves, (2) better achieve the goal of representing and protecting habitat for *all* late-successional associated taxa, and (3) to insure compliance with the National Forest

Management Act's provision that flora and fauna be well distributed within planning units (National Forests in this case). The latter two reasons provide incentive for us to compare the predicted habitat map for the forest carnivores (owl and fisher) developed here with maps developed using similar methods for disparate taxa including rare, late-successional associated terrestrial mollusks and salamanders (Dunk et al., 2004; Welsh et al., 2006). We plan to contrast the optimal selection of habitat for the highly mobile predators included here with the slow-moving species of small vertebrates and rare and locally endemic invertebrates that share a general association with old forest conditions (unpublished data). Furthermore, we will use MARXAN to evaluate the results of single-species models for each species (i.e., fisher, spotted owl, each species of mollusk and salamander), to generate a new system of priority locations for this collection of disparate taxa. This system will then be compared with the system of Late-Successional Reserves, to determine how well it achieves the goal of protecting habitat for wide-ranging endothermic forest predators as well as taxonomically and ecologically disparate group of ecothermic animals.

Balancing the goals of geographic distribution of reserves, and selecting reserves to maintain populations of individual species of concern (e.g., fishers, spotted owls) may require that the current Late-Successional Reserves network be augmented with new priority areas in high-value habitat areas in the most productive low- to mid-elevation forests of the west-central portion of our study. However, with 41% of the federal lands in our study area already designated as either Wilderness or Late-Successional Reserves, some groups might advocate the relocation of current Late-Successional Reserves (adaptive conservation management) rather than adding reserves. The current system is viewed by some as already making too much land unavailable for timber harvest and other activities that may not be compatible with protection of old forest ecosystems. It is important to realize, however, that although about 40% of *federal* lands have some form of protection, a significantly smaller proportion of *all* forest lands in northwestern California are in reserves. Given the public trust duties for wildlife, the federal lands play a unique role in protecting biodiversity, including providing habitat for the area-limited focal species such as the spotted owl and the fisher.

Future planning for focal species in this region should not only include a suite of species that represent a variety of ecological scales and processes but should also include site-selection processes that are based on local habitat models. Ideally, future models should address viability and should be linked with forest growth and change simulators so that planning for long time horizons can include the changes that will occur in forest habitats over time. And, it would be preferable if this goal could be achieved by including lands in *all* ownerships within the range of the constituent species, unlike our analysis which was limited to only federal lands. Finally, we reiterate the sentiments of Margules and Pressey (2000) in that "reserve selection algorithms are only part of an explicit, defensible planning process, not the process itself" and that they operate as only one part of a more complex decision support system with social as well as biological inputs.

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