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**Rocky Mountain
Research Station**

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Multi Scale Habitat Relationships of *Martes americana* in Northern Idaho, U.S.A.

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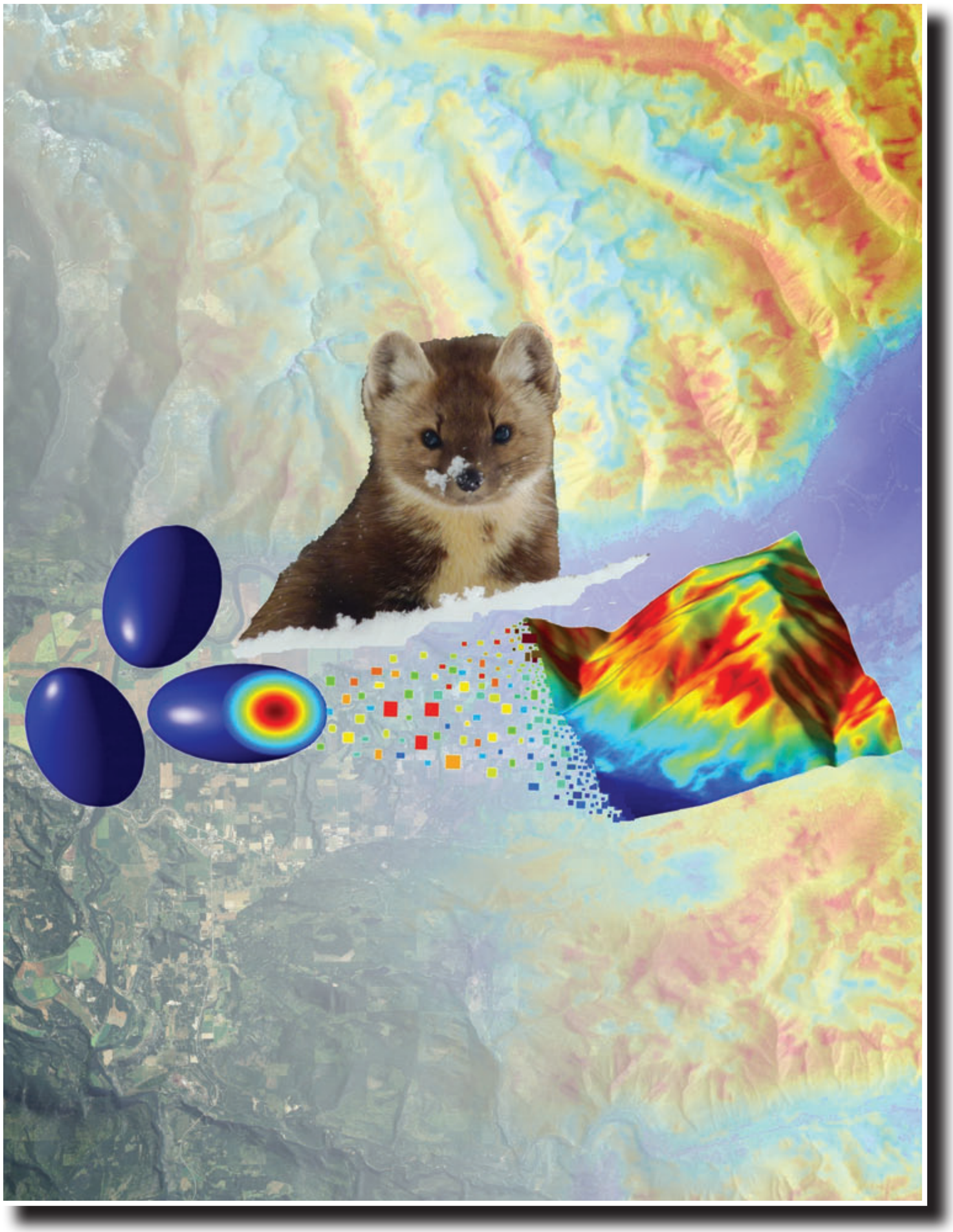

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ABSTRACT

We used bivariate scaling and logistic regression to investigate multiple-scale habitat selection by American marten (*Martes americana*). Bivariate scaling reveals dramatic differences in the apparent nature and strength of relationships between marten occupancy and a number of habitat variables across a range of spatial scales. These differences include reversals in the direction of an observed association from positive to negative and frequent dramatic changes in the apparent importance of a habitat variable as a predictor of marten occurrence. Logistic regression on the optimally scaled input variables suggests that at the scale of home ranges, marten select landscapes with high average canopy closure and low fragmentation. Within these low fragmented landscapes, marten select foraging habitat at a fine scale within late-seral, middle-elevation mesic forests. In northern Idaho, optimum American marten habitat, therefore, consists of landscapes with low road density, low density of non-forest patches with high canopy closure, and large areas of middle-elevation, late successional mesic forest. Comparison of current landscape conditions to those expected under the historic range of variability indicates that road building and timber harvest in the past century may have substantially reduced the amount of suitable marten habitat in northern Idaho. Our results are generally consistent with previous research in the Rocky Mountains, with additional insights related to the relative importance, functional form, and scale at which each habitat variable has the largest influence on marten occurrence.

Keywords: *Martes americana*, multi scale, habitat modeling, logistic regression

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Introduction

The influence of changes in spatial scale on observed pattern-process relationships is a central question in ecology (Levin 1992). Each process may be driven by multiple factors, each acting at different characteristic scales, and apparent pattern-process relationships may change fundamentally across scale (Wiens 1989). It is critical not only to identify correct mechanisms, but also the correct scales at which they act. Failure to do so often results in failure to observe an effect when in fact one exists, observation of spurious effects that are incorrect, or misconstrual of the nature or strength of the pattern-process relationship (e.g., Thompson and McGarigal 2002).

Scaling analysis is particularly important in species-environment relationship analysis. Animals often hierarchically select habitats; therefore, it is important to evaluate habitat selection at a range of spatial scales in order to reveal the true grain at which the animal responds within the landscape (Kotliar and Wiens 1990). Thompson and McGarigal (2002) demonstrated the sensitivity of apparent species-environment relationships to grain, extent, and thematic resolution of habitat variables. The authors observed that bald eagles (*Haliaeetus leucocephalus*) select different habitat variables at widely divergent scales; and incorrect specification of the grain, extent or habitat definition could lead to incorrect conclusions about the habitat relationships of this species. Importantly, the environmental variables of importance and grain of response for some processes, such as establishing home ranges, may differ greatly from the variables and scales of importance for other processes, such as habitat selection for foraging within home ranges.

The information theoretic approach has become the dominant paradigm for use in wildlife habitat selection studies (Burnham and Anderson 2002; Johnson and Omland 2004). Although the advantages of this approach have been extensively reviewed, very little attention has been given to scaling issues when selecting variables for inclusion in candidate models. For most species, information is available to guide decisions regarding appropriate variables for inclusion in candidate models. However, the effect of a given variable on habitat selection may manifest itself at spatial scales ranging from a few meters to kilometers (e.g., Thompson and McGarigal 2002; Grand and others 2004). Most habitat selection studies fail to address this issue and simply evaluate alternative models that are based on predictor variables from a single, arbitrarily selected scale.

For most environmental variables, there is no advance way to know the spatial extent surrounding the sample point at which the variable is most strongly related to species presence. Therefore, it is best to measure each environmental variable across a range of radii surrounding each sampled plot to determine the scale at which each predictor variable is most related to the response. Bivariate scaling (Thompson and McGarigal 2002; Grand and others 2004) has been shown to be a highly effective method for identifying the appropriate scale in species-environment relationship modeling. Characterizing the landscape surrounding each point at multiple scales facilitates the selection of the appropriate scale at which each aspect of landscape composition was most significant for our focal species.

American marten (*Martes americana*) have been shown to be particularly sensitive to fragmentation of late seral forest habitats by road building and timber harvest. Perturbations such as timber harvest remove canopy cover, reduce coarse woody debris, change mesic sites into xeric sites, remove riparian dispersal zones, and change prey communities (Buskirk and Ruggiero 1994). Previous studies have revealed that marten respond to small amounts of forest fragmentation and rarely use sites where more than 25% of forest cover was removed (Hargis and others 1999). Highly contrasted edges and areas of open canopy are strongly avoided by American marten (Buskirk and Ruggiero 1994; Hargis and others 1999). However, previous habitat relationship studies on the species have not thoroughly considered scaling issues in habitat selection. The objectives of this study are: to identify the variables that most strongly influence habitat selection by American marten in northern Idaho and the scale at which each of these variables is most important, and to predict the probability of marten occupancy across a large, mountainous landscape.

Materials and Methods

Study Area

The study area is a 3000-km^2 section of the Selkirk, Purcell, and Cabinet Mountains, encompassing the Bonners Ferry and Priest River Ranger Districts of the Idaho Panhandle National Forest (IPNF; Figure 1). The topography is mountainous, with steep ridges, narrow valleys, and many cliffs and cirques at the highest elevations. Elevation ranges from approximately 700 m to 2400 m above sea level. The climate is characterized by cold, wet winters and mild summers. The area is heavily forested, with subalpine fir (*Abies lasiocarpa*) and Engelmann Spruce (*Picea engelmannii*) codominant above 1300 m, and a diverse mixed forest of Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), ponderosa pine (*Pinus ponderosa*), western white pine (*Pinus monticola*), grand fir (*Abies grandis*), western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), western larch (*Larix occidentalis*), paper birch (*Betula papyrifera*), quaking aspen (*Populus tremuloides*), and black cottonwood (*Populus trichocarpa*) dominating below 1300 m.

Data Collection

Hair snares were set along transects across the portions of the study area during the winter months of January through March in 2005, 2006, and 2007. Transects were selected to

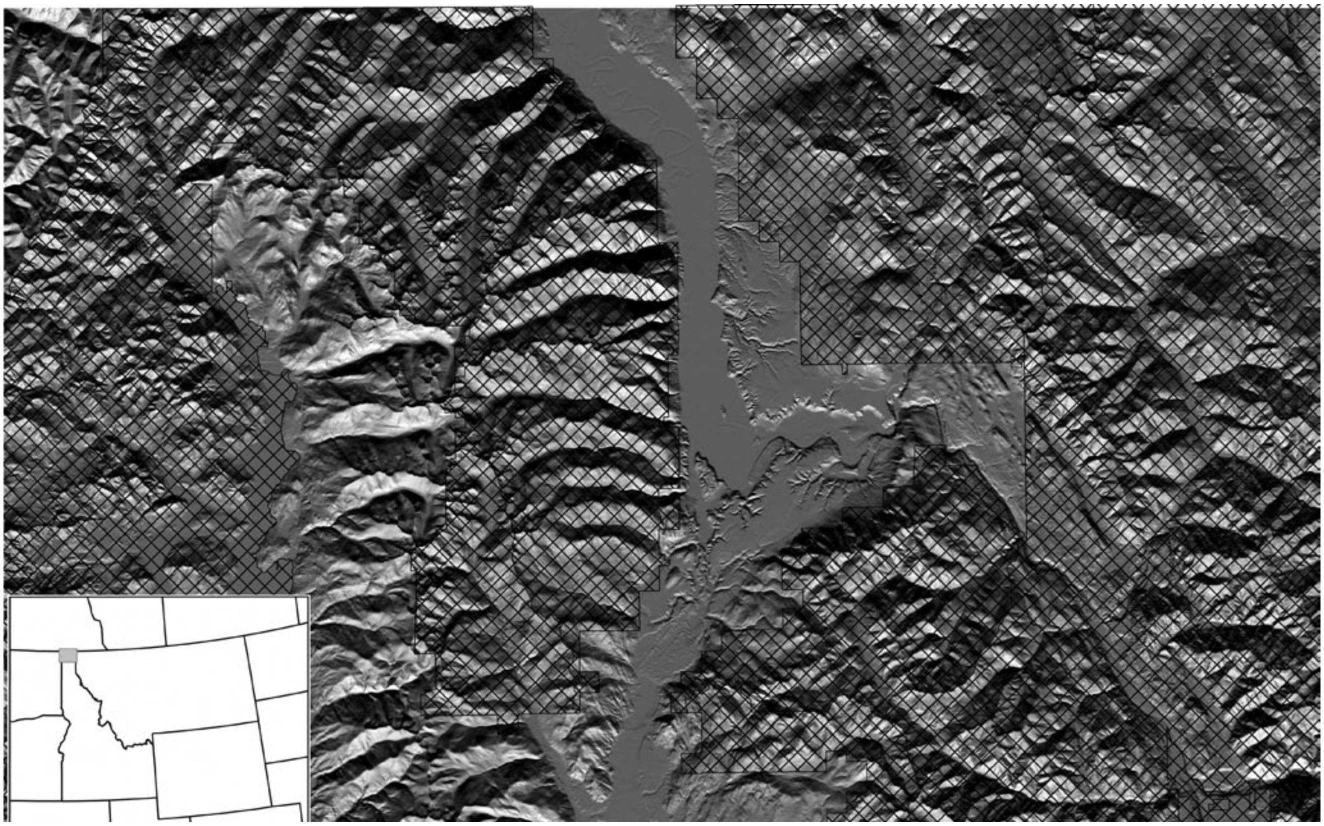


Figure 1. Study area orientation map. Idaho Panhandle National Forest located in northern Idaho, U.S.A.

provide near complete sample coverage across all areas of Federal or State ownership that are accessible with a snowmobile. Each snare consisted of a 1 m x 1 m corrugated plastic sheet folded into an equilateral triangular tunnel with hardware cloth mesh wired to the back end of the snare, creating a one-way opening (Cushman and others 2008; Figure 2). Snares were baited with a ~30 cm^3 cube of deer meat and ~1 tsp beaver castor. Approximately ¼ tsp Gusto, a commercial call lure (Minnesota Trapline Products), was also dabbed onto a sponge and hung above the trap. Each trap was lined with five 30-caliber rifle bore brushes to non-invasively obtain hair samples from animals visiting the snare. Snares were set for two weeks, after which each station was revisited to collect hair samples and re-bait for another two-week cycle. During the check, brushes with hair were removed from the trap and put into sterile tubes filled with desiccant. Each brush is considered a single sample.

All genetic analysis was conducted by the U.S. Forest Service Wildlife Conservation Genetics Laboratory in Missoula, Montana. Hair samples taken from each brush were genetically analyzed at both the species and individual level. Mitochondrial DNA was extracted from hair samples using Qiagen tissue protocols with slight modifications (Mills and others 2000) and amplified with polymerase chain reaction (PCR). Following DNA amplification, PCR products were digested in three restriction reactions with *Hinf*I, *Hae*III, and *Mbo*I (Riddle and others 2003). This method allows the discrimination of mustelid species from all other species. Species identification was determined using diagnostic restriction enzyme patterns followed by amplification of a region of cytochrome b on mitochondrial DNA (Riddle and others 2003). Over the three winter seasons of 2005, 2006, and 2007, 361 locations were surveyed. American marten were detected at 159 individual hair snare stations.

Variable Selection

In advance, we selected several variables we believed would be strongly related to American marten occurrence based on previous research (Buskirk and Ruggiero 1994; Hargis and others 1999; Tomson 1999): elevation, percent canopy closure, road density, patch density, percentage of the landscape occupied by late seral forests, percentage of the landscape occupied by non-stocked clear-cuts, and probability of occurrence of western red cedar (*Thuja plicata*). All input variables were co-rectified to a UTM projection with 30-m cell size.

Elevation

Elevation source data were from the 30-m^2 Shuttle Topographic Radar Mission (Rabus and others 2003) downloaded from the United States Geological Survey (USGS) national map (http://nationalmap.gov). The effects of elevation on the probability of marten occurrence were modeled

Figure 2. Non-invasive hair snare station with five gun brushes, bait, and mesh wire at back to create a one-way opening.

as Gaussian functions on the expectation that martens should show a unimodal optimum in habitat quality with respect to elevation. We evaluated 72 Gaussian elevation variables, consisting of a factorial of 9 levels of elevation (1200 m-2000 m) and 8 levels of standard deviation (300 m-1000 m in 100-m increments (e.g., Cushman and others 2006).

Landcover

We created a consistent seral stage layer by merging the IPNF stands map (R1 TSMRS handbook, Art Zack, pers. comm.) with the Idaho Department of Lands Timber Type map (IDL 2006) after confirming a comparable cross-walk of diameter at breast height (DBH) size classes. Final classes in the seral stage map and their descriptions are found in Table 1.

We calculated landscape composition and configuration variables for 11 focal landscape extents surrounding each marten sampling station using FRAGSTATS (McGarigal and others 2002). The variables consisted of one landscape-level metric characterizing the mosaic of cover types and two class-level metrics characterizing a focal cover type (Table 2). We chose patch density (PD) as a landscape-level metric due to previous work showing that marten avoid fragmented landscapes (Hargis and others 1999). The class-level metrics were only calculated for particular cover classes thought to be important in influencing species distribution (Buskirk and Powell 1994). Specifically, we calculated the percentage of the focal landscape (PLAND) for the large size class, as past work has shown strong effects of the area of late seral forests on the probability of

Table 1. Vegetation and timber classification on both State and Federal lands in the study area. Seral stage is presented with DBH in cm.

Class	Description
1. Large sawtimber	Dominant and codominant trees with DBH>40.6 cm
2. Small sawtimber	Dominant and codominant tress with DBH 20.3-40.6 cm
3. Pole timber	Dominant and codominant trees with DBH 7.62-20.3 cm
4. Seedling/sapling	Crop trees <1.37 m and <7.62 DBH (open canopy)
5. Non-stocked	Forest land less than 10% stocked with growing trees
6. Non-forest	Non-forested areas

Table 2. List of final predictor variables used in logistic regression models after univariate analyses.

Predictor variable	Most significant scale (m)	Variable acronym
Elevation	1400, s.d. 400	el4s.x14
All Roads	1980	ar1980
Percent Canopy Closure to 4th power	990	canopy4xs_990
Western Red Cedar	90	thpl
Patch Density (landscape level)	990	pd990
PLAND Large Sawtimber (Class 1)	90	pland190
PLAND Non-stocked Areas (Class 5)	990	pland5990

marten occurrence (Hargis and others 1999). Likewise, we calculated percentage of the landscape for non-stocked seral stage consisting of unregenerated past timber harvest areas, as past work has shown marten avoid landscapes with even moderate amounts of recent clear-cuts (Hargis and others 1999). All metrics were derived at 11 scales using circular windows with radii window sizes from 90 m to 990 m in 90-m increments around each sample point with FRAGSTATS (McGarigal and others 2002).

Canopy Closure

Canopy closure was taken from the National Land Cover Data canopy closure layer (NLCD 2001). We calculated focal mean percent canopy across 11 scales ranging from 90 m radius to 990 m radius in 90-m increments around each point. We produced 88 functionally scaled surfaces for canopy closure by transforming the focal mean layers with 8 power functions expressing alternative hypothetical response curves of marten habitat suitability as a function of canopy closure: the linear and power functions of 0.2, 0.4, 0.6, 0.8, 2nd, 3rd, and 4th power (Figure 3). These curves collectively describe a broad range of potential changes in marten habitat suitability across canopy closure, including non-linear threshold relationships.

Road Density

We used two forms of the roads layer (Cushman and others 2006), one depicting only roads that are currently maintained, and one depicting so-called "ghost" roads that do not appear on current travel maps and include abandoned roads in various stages of recolonization by vegetation. We calculated the density of roads within focal landscapes centered on each marten detection station at 12 scales ranging from 90 m to 1980 m in 180-m intervals around each sample point.

Cedar Forest Type

The site suitability for western red cedar was derived for each marten detection station from species probability maps. We selected this species as a predictor of marten occurrence given the strong associations of marten in northern Idaho with mesic, riparian forest types (Tomson 1999). These maps were created using a random forest ensemble modeling approach based on climatic, topographic, and spectral predictor variables (Evans and Cushman 2009).

Bivariate Scaling

The first step in the analysis is bivariate scaling (Thompson and McGarigal 2002; Grand and others 2004) to identify the scale at which each independent variable is most strongly related to American marten occurrence. We used a non-parametric difference in means test (PROC NPAR1WAY Wilcoxon; SAS Institute 1999-2000; Grand and others 2004) to evaluate the nature and strength of relationship between each environmental variable and marten

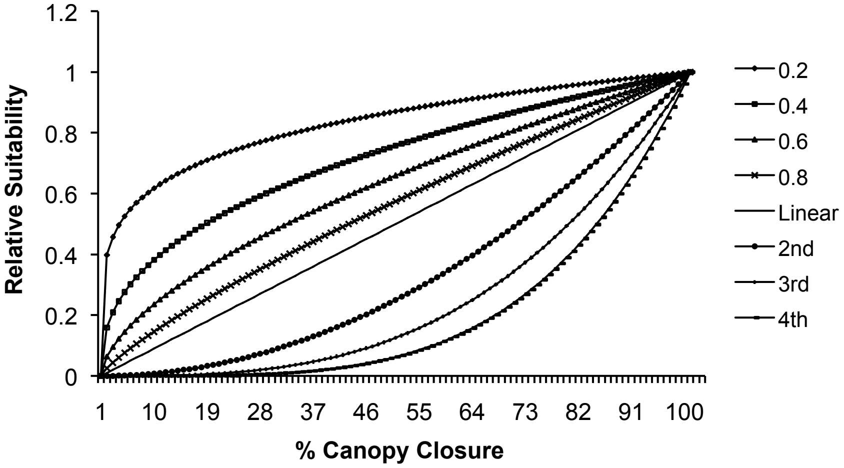


Figure 3. Power functions transforming predicted habitat suitability as a function of canopy closure. We evaluated eight power transformations ranging from 0.2 to 4th power.

occurrence across the spatial scales previously described. We evaluated the sensitivity of the apparent relationship between each variable and marten occurrence to changes in focal scale and identified the scale at which each variable was most highly related to marten occurrence. We selected the scale producing the smallest p-value less than 0.05 and excluded all other scales of each variable from further analysis. After this scale selection process was completed, we eliminated one of each pair of variables with a Pearson's correlation greater than 0.5.

Logistic Regression Analysis

We used an all-subsets approach to test all combinations of our seven variables (Table 3). We used model averaging based on AIC weights to produce parameter estimates for a final model. To assess model predictive ability, we used the max-Kappa cut-point to calculate percent of observations correctly classified, sensitivity, and specificity. We computed Cohen's Kappa statistic, percent observations correctly classified, and area under the Receiver Operating Characteristic (ROC) curve—known as the "area under curve" (AUC). We computed variance inflation factors for all variables in the model. We computed the significance of each variable in the model with Wald statistics. We checked for over-dispersion by computing the ratio of residual scaled deviance to the residual degrees of freedom.

We measured the effects sizes of the variables in the final model by calculating probability of marten presence as each variable ranged from the 10th to the 100th percentile of values in the sampled dataset, while holding all other variables constant at their medians. We calculated the AIC variable importance of each variable by summing the AIC model weights of all models that included each variable.

Results

Bivariate Scaling

The bivariate scaling analysis revealed that the strength and nature of observed relationships between marten occurrence and all measured environmental variables is highly dependent on the focal scale within which the variable is derived.

Landscape Fragmentation Metrics

We produced bivariate scaling plots for the landscape fragmentation metric Patch Density. The highest degree of support was at the largest focal landscape scale of 990 m, with p-value less than 0.005, indicating strong association between Patch Density and marten occurrence at broad spatial scales (Figure 4). Also, the strength of the observed relationship with these variables was highly scale dependent, with non-significant relationships at the 0.05 level when calculated at the finest scale of 90-m focal landscape. American marten in the study area occur more frequently in landscapes with low density of patches, indicative of unfragmented landscapes dominated by large and contiguous patches.

Landscape Composition Metrics

We produced bivariate scaling plots for two landscape composition metrics: Percentage of Landscape (PLAND 1; Figure 5) for the late seral forest class, and Percentage of the Landscape in non-stocked (clear-cut and recent fire) class (PLAND 5; Figure 6). Scaling suggests significant positive relationships between marten occurrence and area of late seral forest at the finest (90 m) scale tested. There were highly significant negative associations with landscape area in non-stocked cover types across all 11 tested focal landscape scales. This metric also showed two peaks of support, with very highly significant negative association between marten occurrence and area of non-stocked cover type at 360 m and 990 m radius focal landscape.

Road Density

We evaluated two forms of the road data: roads that are maintained in drivable condition (Open Roads), and All Roads, including so-called abandoned and unmaintained "ghost" roads that don't appear in current travel maps but still remain in varying levels of regeneration in the landscape (Figure 7). There was a clear difference between the two forms of road data, with the All Roads form having lower p-value (stronger relationship) at all spatial scales. Marten detection was most strongly affected by road density at the broadest scale tested, corresponding to focal landscapes with 1980-m radius.

Canopy Closure

We evaluated the relationship between marten occurrence and canopy closure across 88 combinations of focal landscape extent and power transformation of percent canopy closure. This bivariate scaling indicated a strong peak in significance at the broadest landscape extent tested, with martens positively associated with high amounts of average canopy closure at a 990-m radius focal landscape scale (Figure 8). There was relatively little difference among power transformations (Figure 3) of canopy closure and marten occurrence, with marginally higher support for canopy closure to the 4^{th} power compared to the other transformations.

Elevation

We evaluated 72 Gaussian elevation variables consisting of a factorial combination of nine levels of mean elevation and eight levels of standard deviation. Bivariate scaling revealed very strong positive association with the Gaussian elevation index with mean of 1400 m and a 400-m standard deviation. There was relatively little differentiation among different standard deviations of the elevation relationship compared to the strong differentiation among mean elevations.

Table 3. Models, AICc, and AIC model weights for all candidate models with non-zero AIC weights. The variable acronyms correspond to those give in Table 2. Delta—difference in AICc between the model on that line and the model with the lowest AICc; wi—AIC weight of the model on that line.

Model	AICc	Delta	wi
canopy4xs_990+ar1980+el4s.x14+thpl+pland5990	469.539	0	0.087834
canopy4xs_990+ar1980+el4s.x14+thpl+pd990+pland5990	469.644	0.105	0.083341
canopy4xs_990+el4s.x14+thpl+pd990+pland5990	470.317	0.778	0.059528
canopy4xs_990+ar1980+el4s.x14+thpl+pland5990+pland190	470.841	1.302	0.045807
canopy4xs_990+el4s.x14+pd990+pland5990	470.997	1.458	0.04237
canopy4xs_990+ar1980+el4s.x14+pd990+pland5990	471.083	1.544	0.040587
canopy4xs_990+ar1980+el4s.x14+thpl+pd990	471.09	1.551	0.040445
canopy4xs_990+ar1980+el4s.x14+thpl+pd990+pland5990+pland190	471.225	1.686	0.037805
canopy4xs_990+ar1980+el4s.x14+pland5990	471.29	1.751	0.036596
canopy4xs_990+el4s.x14+thpl+pd990	471.291	1.752	0.036578
canopy4xs_990+el4s.x14+thpl+pd990+pland5990+pland190	471.388	1.849	0.034846
canopy4xs_990+ar1980+el4s.x14+thpl	471.768	2.229	0.028816
canopy4xs_990+el4s.x14+thpl+pland5990	471.957	2.418	0.026218
canopy4xs_990+el4s.x14+thpl+pd990+pland190	472.064	2.525	0.024852
canopy4xs_990+el4s.x14+pd990+pland5990+pland190	472.159	2.62	0.023699
canopy4xs_990+el4s.x14+pd990	472.197	2.658	0.023253
canopy4xs_990+el4s.x14+thpl+pland5990+pland190	472.28	2.741	0.022308
canopy4xs_990+ar1980+el4s.x14+thpl+pd990+pland190	472.381	2.842	0.021209
canopy4xs_990+ar1980+el4s.x14+pland5990+pland190	472.581	3.042	0.019191
canopy4xs_990+ar1980+el4s.x14+thpl+pland190	472.622	3.083	0.018802
canopy4xs_990+ar1980+el4s.x14+pd990+pland5990+pland190	472.669	3.13	0.018365
canopy4xs_990+ar1980+el4s.x14+pd990	472.687	3.148	0.0182
canopy4xs_990+el4s.x14+pland5990	472.758	3.219	0.017566
canopy4xs_990+el4s.x14+pd990+pland190	473.073	3.534	0.015006
canopy4xs_990+el4s.x14+pland5990+pland190	473.191	3.652	0.014146
canopy4xs_990+el4s.x14+thpl+pland190	473.495	3.956	0.012151
canopy4xs_990+el4s.x14+thpl	473.664	4.125	0.011167
canopy4xs_990+ar1980+el4s.x14	473.747	4.208	0.010713
canopy4xs_990+ar1980+el4s.x14+pd990+pland190	473.987	4.448	0.009501
canopy4xs_990+thpl+pd990+pland5990+pland190	474.577	5.038	0.007074
canopy4xs_990+ar1980+el4s.x14+pland190	474.586	5.047	0.007042
canopy4xs_990+pd990+pland5990+pland190	474.605	5.066	0.006976
canopy4xs_990+ar1980+thpl+pd990+pland5990	474.663	5.124	0.006776
canopy4xs_990+el4s.x14+pland190	474.689	5.15	0.006689
canopy4xs_990+pd990+pland5990	474.719	5.18	0.006589
canopy4xs_990+el4s.x14	474.745	5.206	0.006504
canopy4xs_990+thpl+pd990+pland5990	474.937	5.398	0.005909
canopy4xs_990+ar1980+thpl+pd990+pland5990+pland190	474.98	5.441	0.005783
canopy4xs_990+ar1980+pd990+pland5990	475.016	5.477	0.00568
canopy4xs_990+ar1980+pd990+pland5990+pland190	475.476	5.937	0.004513
canopy4xs_990+ar1980+thpl+pland5990+pland190	475.661	6.122	0.004114
ar1980+el4s.x14+thpl+pd990+pland5990	476.07	6.531	0.003353
canopy4xs_990+ar1980+thpl+pland5990	476.194	6.655	0.003152
canopy4xs_990+ar1980+pland5990+pland190	476.391	6.852	0.002856
el4s.x14+thpl+pd990+pland5990	476.479	6.94	0.002733
canopy4xs_990+thpl+pland5990+pland190	476.634	7.095	0.002529

Table 3. *Continued*.

Model	AICc	Delta	wi
canopy4xs_990+pland5990+pland190	476.725	7.186	0.002417
canopy4xs_990+ar1980+pland5990	476.768	7.229	0.002365
ar1980+el4s.x14+thpl+pland5990	476.808	7.269	0.002319
el4s.x14+thpl+pd990+pland5990+pland190	477.415	7.876	0.001712
ar1980+el4s.x14+thpl+pd990+pland5990+pland190	477.534	7.995	0.001613
canopy4xs_990+thpl+pd990+pland190	477.576	8.037	0.001579
el4s.x14+pd990+pland5990	477.587	8.048	0.001571
canopy4xs_990+pd990+pland190	477.738	8.199	0.001456
ar1980+el4s.x14+thpl+pland5990+pland190	477.864	8.325	0.001367
ar1980+el4s.x14+pd990+pland5990	477.95	8.411	0.00131
canopy4xs_990+pland5990	478.409	8.87	0.001041
el4s.x14+thpl+pd990	478.547	9.008	0.000972
canopy4xs_990+thpl+pland5990	478.628	9.089	0.000933
ar1980+el4s.x14+thpl+pd990	478.637	9.098	0.000929
el4s.x14+pd990+pland5990+pland190	478.638	9.099	0.000929
canopy4xs_990+ar1980+thpl+pd990+pland190	478.687	9.148	0.000906
canopy4xs_990+pd990	478.969	9.43	0.000787
el4s.x14+thpl+pd990+pland190	479.013	9.474	0.00077
canopy4xs_990+thpl+pd990	479.11	9.571	0.000733
el4s.x14+thpl+pland5990+pland190	479.165	9.626	0.000714
canopy4xs_990+ar1980+pd990+pland190	479.182	9.643	0.000707
ar1980+el4s.x14+pland5990	479.194	9.655	0.000703
el4s.x14+thpl+pland5990	479.233	9.694	0.00069
ar1980+el4s.x14+pd990+pland5990+pland190	479.425	9.886	0.000627
canopy4xs_990+ar1980+thpl+pd990	479.638	10.099	0.000563
ar1980+el4s.x14+thpl+pd990+pland190	479.646	10.107	0.000561
el4s.x14+pd990	479.687	10.148	0.00055

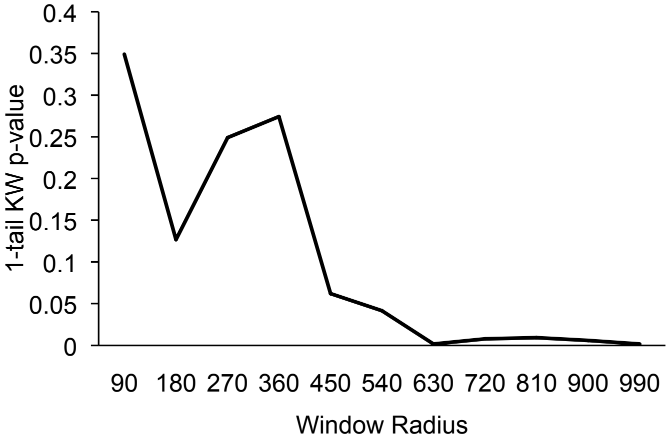


Figure 4. Bivariate scaling plot of 1-tail Kruskal-Wallis p-value for relationship between marten occurrence and landscape-level patch density. The graph indicates highly significant association of marten with low patch density at spatial scales above 450, with highest support at the largest focal extent tested, 990 m.

Figure 5. Bivariate scaling plot of 1-tail Kruskal-Wallis p-value for relationship between marten occurrence and percentage area in late seral forest cover across 11 spatial scales. The graph indicates significant association between marten occurrence and area of late seral forest in a focal landscape at scales from 90 m up to 450 m, with the strongest relationship at the smallest window size tested, 90 m.

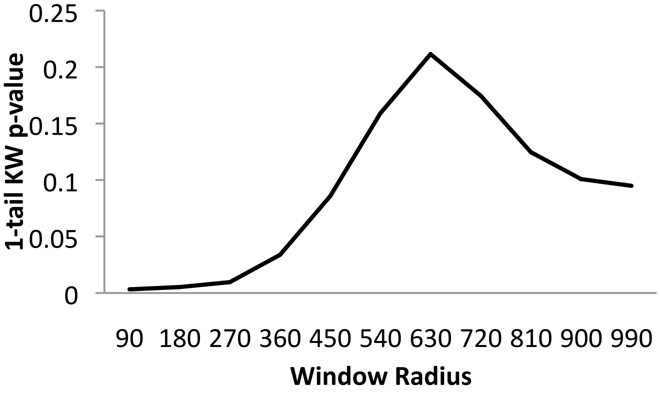


Figure 6. Bivariate scaling plot of 1-tail Kruskal-Wallis p-value for relationship between marten occurrence and percentage area in the non-stocked cover type across 11 spatial scales The graph shows significant negative effect of area of non-stocked clear-cuts in the focal landscape surrounding detection stations at all scales tested, with the highest effect at the largest window size tested, 990 m.

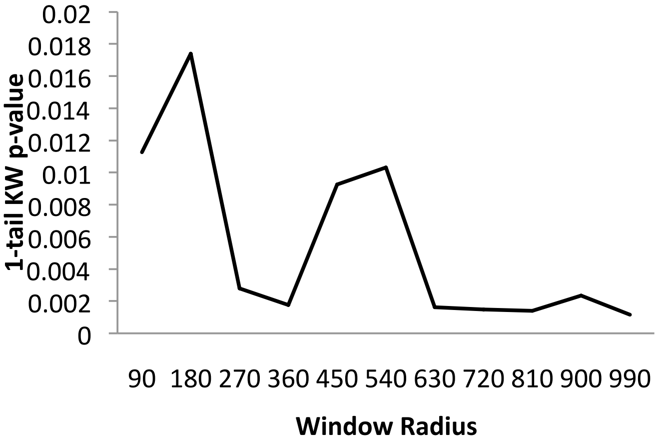
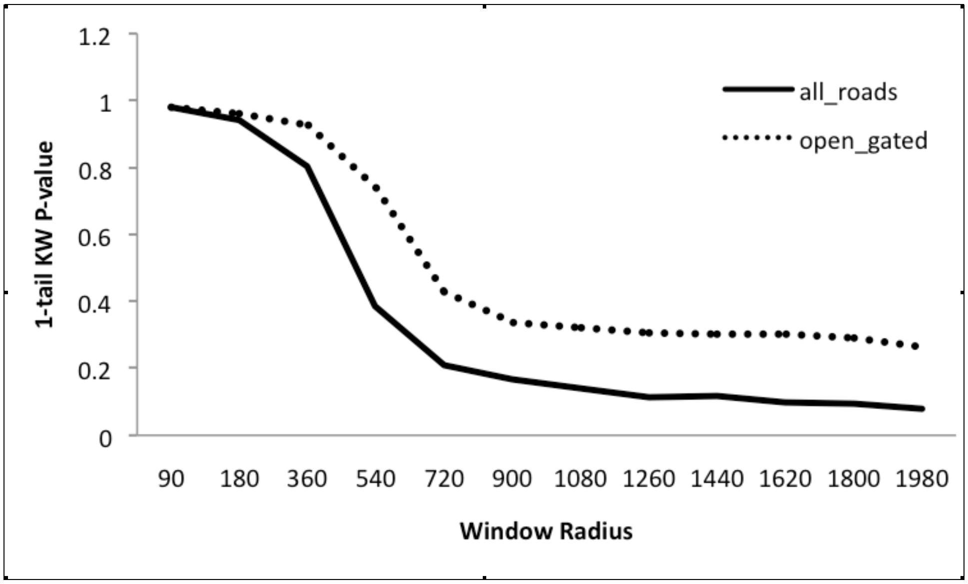


Figure 7. Bivariate scaling plot of 1-tail Kruskal-Wallis p-value for relationship between marten occurrence and road density across 12 spatial scales. All Road—maintained, unmaintained, and abandoned roads; Open Road—maintained roads. The figure shows a stronger negative effect of road density of all roads than maintained roads across all scales evaluated. The graph also shows the largest negative effect of road density on marten occurrence at the largest window size tested, 1980 m.



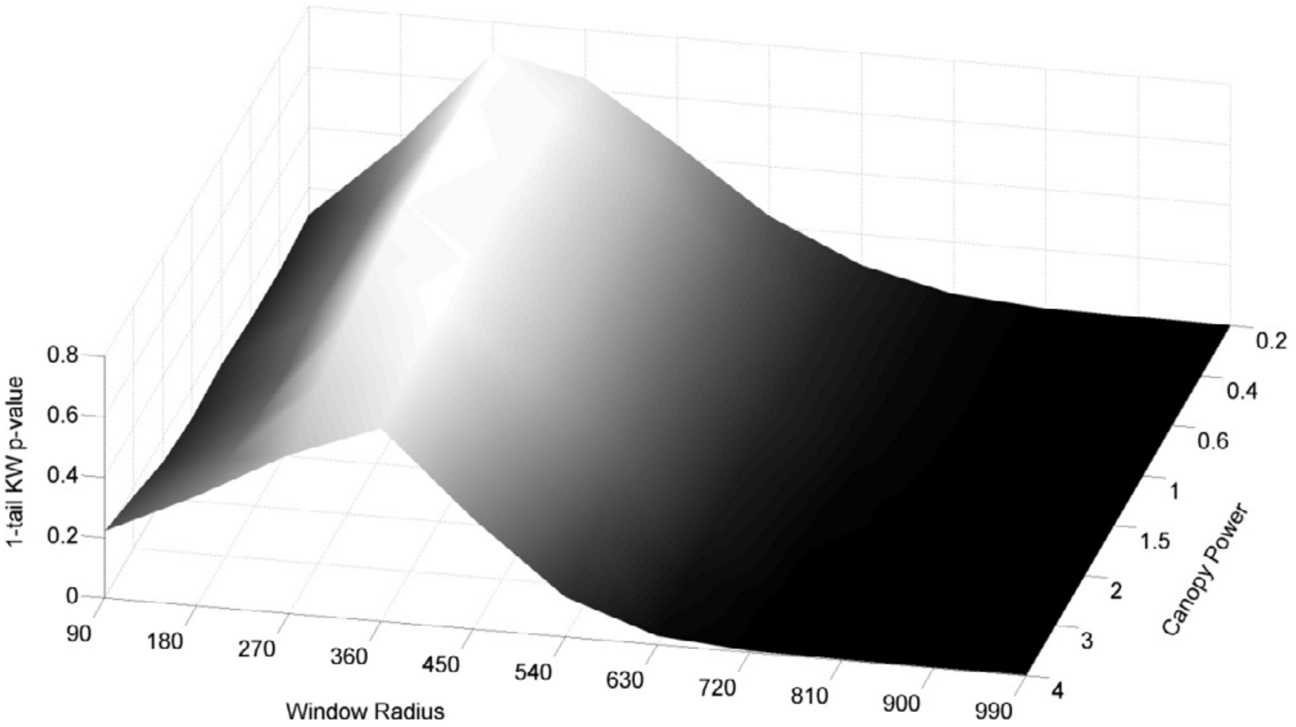


Figure 8. Bivariate scaling factorial for 88 combinations of focal landscape window radius and mean canopy closure transformed by 8 power functions (Figure 2). The surface indicates a strong peak of support for a positive relationship between mean landscape canopy closure at a 990-m landscape radius, with marginally higher support for canopy closure to the 4th power than other power transformations.

Logistic Regression Analysis

Following bivariate scaling, there were seven final predictor variables for logistic regression modeling (Table 2). Seventy-three models produced from an all-subsets analysis of predictor variables have non-zero AIC weights, with 11 models within 2 AICc (AIC corrected for small sample size) units of the top model. Thus, the support of the nominally top model as the exclusive basis for interpretation is very low. Thus, we used model averaging based on AIC weights to produce a final averaged model that equitably represents the support for all candidate models (Table 4). The averaged model indicated that occurrence probability for American marten increases with the average percent canopy closure to the 4th power within a 990-m focal radius, percentage of a 90-m focal landscape occupied by late seral forest, and site suitability for western red cedar. Occurrence probability peaked with respect to elevation at 1400 m and 400 m standard deviation. The averaged model indicated that occurrence probability of American marten decreased with density of all roads within a 1980-m focal radius, percentage of 990-m focal radii in non-stocked timber areas, and landscape-level patch density within a 990-m focal radius.

Variable Importance

We assessed variable importance in two ways. First, we calculated the AIC variable importance, which measured the cumulative AIC weight of all models that include a given variable (Table 4). AIC importance value of 1.0 indicates

Table 4. Parameters of final averaged model, AIC variable importance values, and variable effects size. AIC importance values are the sum of AIC model weights for all models that include the variable. The variable effects size (change in P [10%-100%]) is proportional change in probability of detection as the focal variable is changed from the 10th to the 100th percentile of values in the dataset.

	intercept	canopy	roads	elev	cedar	pland5	pd	pland1
Averaged coefficient	-0.30	0.42	-0.11	0.35	0.13	-0.07	-0.20	0.13
Averaged standard error	0.11	0.15	0.12	0.13	0.11	0.22	0.12	0.15
Importance values		1.00	0.59	1.00	0.64	0.57	0.60	0.35
Change in P (10%-100%)		61.05	-53.05	19.78	77.21	-35.99	-46.26	13.21

that the variable is included in all models that have non-zero AIC weight. Values less than one indicate the cumulative AIC weight of all models including that variable. Based on AIC variable importance, canopy closure within a 990-m focal radius and a Gaussian function of elevation with optimum at 1400 m are equally important, with AIC importance value of 1.0. Four other variables had AIC importance values over 0.5, indicating substantial importance in the averaged model. In rank order importance, these variables are: site-level suitability for western red cedar, patch density, road density, and percentage of the landscape within a 990-m focal radius occupied by non-stocked clear-cuts.

Our second measure of variable importance presents the change in probability of marten occupancy as each variable changes from its 10th to 100th percentile in the sample data set, holding all other variables constant at their medians (Table 4). Based on this measure of variable importance, site-level suitability for cedar was identified as the most important variable. Probability of marten occurrence increased 77% as site suitability for cedar rose from its 10th percentile (approximately 23% probability of cedar occurrence) to 100th percentile (approximately 78% probability of cedar occurrence). The second most important variable based on effect size was canopy cover within a 990-m focal landscape. Probability of marten occurrence increased 61% as canopy cover rose from its 10th to 100th percentile (66% to 95% canopy closure). Road density was the third most important variable based on effects size, with marten probability of occurrence decreasing 53% as road density rose from its 10th to 100th percentile. Density of patches of different seral stages in the landscape is the next most important variable based on effects size, with probability of marten occurrence dropping by 46% as patch density changes from the 10th to the 100th percentile of values in our dataset. Similarly, probability of marten occurrence decreases by 36% as the proportion of 990-m radius focal landscape occupied by non-stocked clear cuts rises from the 10th to the 100th percentile. Elevation and percentage of local area occupied by late seral forest were the least important variables based on effects size.

Model Assessment

The final average model was very highly significant based on Wald statistics (Table 5). Three of seven variables in the final model are statistically significant based on Wald scores and p-values at a 0.05 level—(canopy4sx_990, THPL, elev1400). All eight variables had variance inflation factors near 1, indicating no effect of unaddressed collinearity inflating explained variance (Table 5). The ratio of scaled residual deviance to scaled degrees of freedom was 1.2745, indicating little model over-dispersion.

Model Prediction

The Generalized R2 N index of Nagelkerke indicates that approximately 15% of the variance in marten occurrence among sites is accounted for by the model. The AUC is 0.70, indicating that the model performs moderately well in discriminating marten occurrence from non-detection (Figure 9). The model has moderate Percent Correctly Classified (PCC), high specificity, and moderate sensitivity (Table 6; Figure 10). The Kappa statistic indicates that the model discriminates between detections and non-detections 31% better than chance. Figure 11 is a map of predicted habitat quality across the study area produced by applying the final averaged model.

Table 5. Wald statistics and variance inflation factors (VIF) for each variable in the final averaged model.

Factor	Chi-square	P	VIF
canopy4xs_990	7.15	0.0075	1.101
All Roads (ar1980)	2.51	0.1134	1.140
Western Red Cedar (thpl)	3.9	0.0483	1.037
pd990	1.19	0.2758	1.144
pland5990	1.92	0.1655	1.076
pland190	0.41	0.5221	1.125
elev5_m1000	9.83	0.0017	1.129
TOTAL	33.74	<.0001	

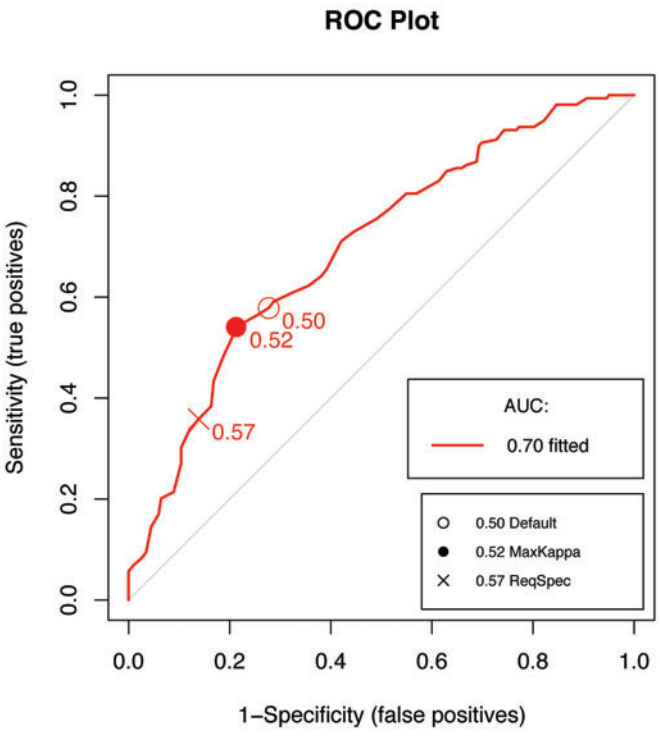


Figure 9. Receiver Operator Characteristic (ROC) plot showing the MaxKappa cutpoint of 0.52 and the area under the ROC curve (0.70) for the final averaged model.

Table 6. Cutpoint threshold, percent of observations correctly classified, sensitivity, specificity, Kappa, and AUC. We present results for two cutpoints: (1) the MaxKappa cutpoint, with a threshold of 0.52, which maximizes the Kappa statistic and PCC; and (2) the default cutpoint of 0.50.

	Threshold	PCC	Sensitivity	Specificity	Kappa	AUC
MaxKappa	0.52	0.678	0.541	0.787	0.335	0.70
Default	0.50	0.659	0.57	0.723	0.303	0.70

Figure 10. Histogram of presence and absence data points along the gradient of predicted probability from 0 to 1. There is a peak of presence points at high predicted probability of occurrence.

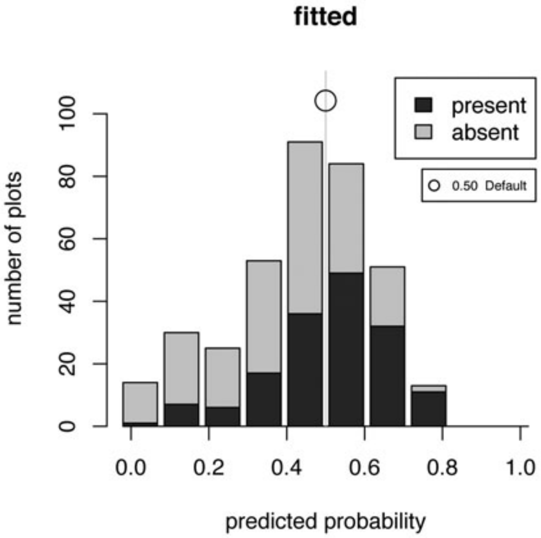
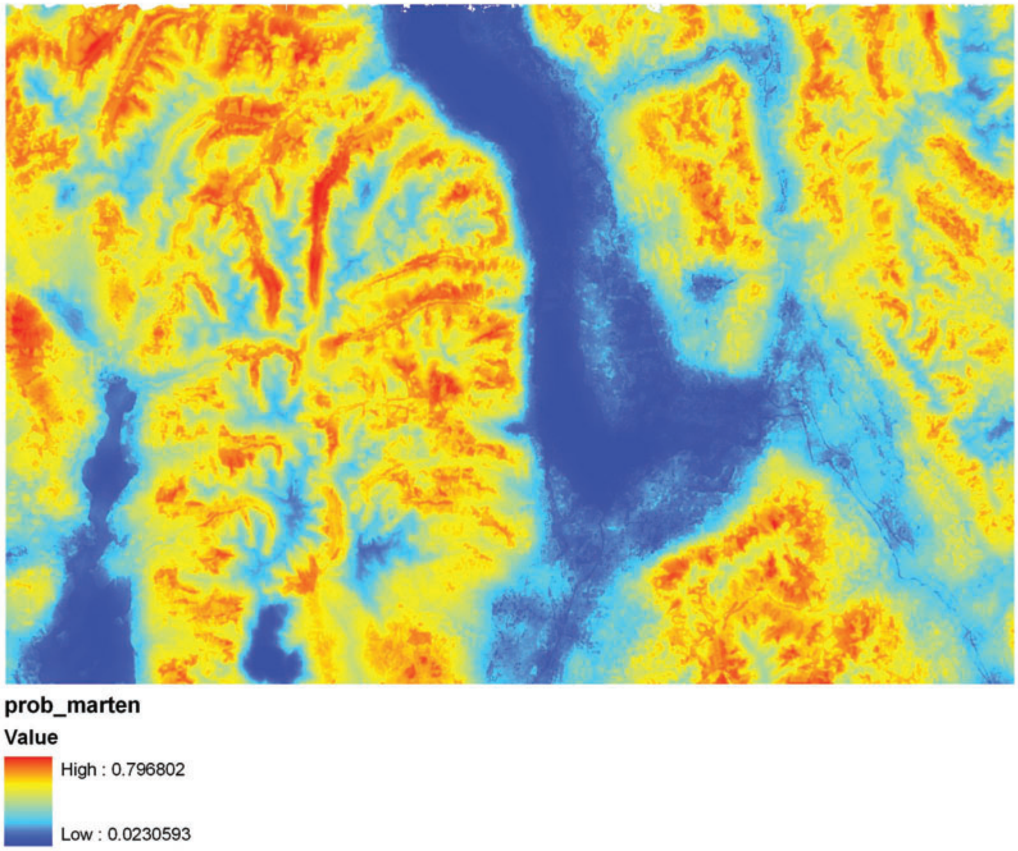


Figure 11. Predicted probability of marten occurrence across the study area as function of the final averaged model.



Discussion

A fundamental concept in animal ecology is that each species occurs within a limited range of environmental conditions, defining its habitat niche (Hutchinson 1957). Most past wildlife habitat relationships modeling has focused on identifying the most important habitat variables. However, in the past several decades, it has become evident that identifying the operative scale for these variables is equally important to the extent that scaling has been proposed as a central question in ecology (Levin 1992). Identifying the proper variables, but at an incorrect scale, may lead to weak or incorrect apparent relationships (Wiens 1989; Thompson and McGarigal 2002; Grand and others 2004). In this analysis, we focused explicitly on evaluating the relationships between American marten occupancy and several potentially important environmental variables across a range of spatial scales.

Scale Dependency of Marten Habitat Relationships

The bivariate scaling analysis revealed high sensitivity of marten habitat relationships to the scale at which habitat variables are measured. We observed strong and consistent relationships with the landscape fragmentation variables, with uniformly positive association of marten occurrence with landscapes that contain high canopy closure, low density, and low area of non-stocked clear-cuts.

The roads scaling analysis revealed two interesting patterns. First, it indicated that unmaintained and closed roads add explanatory power to the road density relationship, indicating the importance of legacy and “ghost” roads to habitat quality for this species. Second, the bivariate scaling analysis for marten revealed that the effects of road density on marten occurrence have a very large spatial range, with habitat quality diminished by road density at distances up to 2 km from a road. This long-distance, diffuse effect suggests that roads can have large cumulative effects that extend across broad landscapes and can reduce habitat quality over large extents.

Bivariate scaling of the relationship between canopy closure and marten occurrence suggested a strong positive association between high levels of canopy closure at a broad landscape scale and marten occurrence. The factorial also indicated higher support for canopy closure to the 4^{th} power (Figure 3), suggesting a non-linear relationship in which habitat suitability decreases rapidly as average canopy closure drops below about 75% at the landscape level. Interestingly, this is very similar to the fragmentation threshold for marten identified by Hargis and others (1999).

Scaling analysis identified a strong peak of association between marten occurrence and elevation, with marten occurrence most likely at 1400 m elevation, with suitability decreasing as a Gaussian function with 400-m standard deviation. Interestingly, marten are commonly assumed to be high-elevation and subalpine forest associated species in the Rocky Mountains. However, our elevation results suggest that this is not the case in northern Idaho, with highest marten suitability in middle-elevation forest in our study area. We hypothesize this may be due to competition with other mustelids (e.g., fisher), forest type and presence of western red cedar, and/or winter snow depth, where higher elevations and deeper snow would prohibit efficient movement of marten across the landscape.

Predicting Habitat Quality and Management Effects

The final averaged model suggested that at scales approximately the size of home ranges within the study area (Wasserman 2008), marten select landscapes with high average canopy closure, low road density, and low forest fragmentation. Importantly, our analysis indicated that American marten respond to canopy closure in a strongly non-linear, threshold-like way (Figure 3), such that habitat suitability within a focal landscape remains quite low until average canopy closure exceeds 40%, with suitability rising rapidly as average canopy closure approaches 100%. Within these low-fragmentation landscapes, marten select foraging habitat at a fine scale within middle-elevation, late-seral, mesic forests, often with a large component of western red cedar. In northern Idaho, optimum American marten habitat, therefore, consists of landscapes with low road density, low density of patches, and low percentage of landscape comprised of non-stocked areas, with high canopy closure and large areas of middle-elevation, late successional forest.

While these generalities are informative, managers need specific guidance regarding targets in desired amounts and configurations of habitat elements at the landscape level. Calculation of change in probability of occurrence across each variable provides a detailed understanding of both the relative effects of each variable in the final model (Table 4; Figures 12-16). This information is useful to managers in order to quantitatively evaluate the probable effects of particular management alternatives on marten habitat suitability at the project and landscape scales.

Biophysical site potential for western red cedar is the variable with the largest effect on marten probability of occurrence (Figure 12). A change from 23% (10^{th} percentile in the dataset) probability of cedar occurrence to 75% (100^{th} percentile in the dataset) probability of cedar occurrence resulted in a 77% increase in the probability of marten occurrence (from ~35% to ~62%). This indicates that American marten favor wet and productive forest types that have high biophysical suitability for the occurrence of western red cedar. Tomson and others (1999) also found that marten habitat use was highest in mesic forest in riparian zones in northern Idaho. However, the very strong association with this mesic, middle-elevation forest type is at odds with the commonly held belief that marten habitat is optimum in late seral, high-elevation forest. Our results suggest that high-elevation forests, such as those dominated by subalpine fir and Engelmann spruce in our study area, are substantially less valuable as habitat to marten.

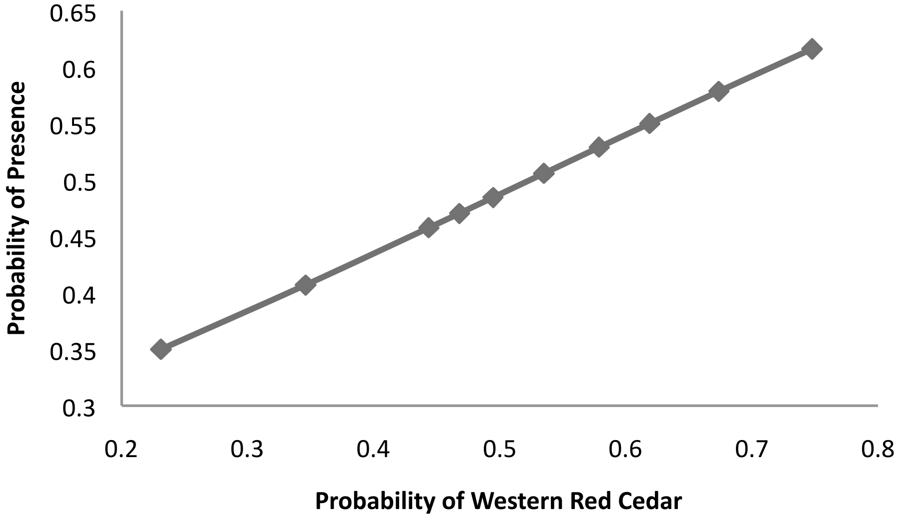


Figure 12. Change in probability of marten detection as the site suitabilty for western red cedar changes from the 10th to the 100th percentile in the database, holding all other variables constant at their medians.

The average canopy cover within a 990-m focal landscape was the variable with the second largest marginal effect on probability of marten detection (Figure 13). An increase in average canopy closure within a 990-m radius focal landscape from its 100th percentile in the database (67% canopy closure) to the 100th percentile in the database (94% canopy closure) results in an increase in the probability of marten detection from 37% to 61%, holding all other variables constant at their medians. This indicates that canopy clover at a broad landscape scale has very strong associations with marten occurrence. This broad scale effect suggests that marten select home ranges within landscapes with high canopy cover at scales at of 1 km or larger.

The density of all roads at the broadest landscape scale tested (1980 m) was the third strongest predictor variable based on effects size (Figure 14). An increase in road density from 1.1 km per km^2 (10th percentile) to 7.2 km per km^2 (100th percentile) resulted in a decrease in probability of marten occurrence from 53% to 35%. This shows substantial effects of road density at very broad landscape extents on the probability of marten occurrence. Importantly, our analysis found that the density of all roads, including those closed and abandoned up to several decades in the past, was a higher predictor of marten occurrence than currently maintained roads. This emphasizes the import effects of these so-called “ghost” roads on landscape fragmentation and wildlife habitat suitability.

Landscape fragmentation, as measured by Patch Density, was the variable with the fourth largest effects size (Figure 15). Specifically, probability of marten occurrence decreased from 56% to 32% as patch density increased from its 10th percentile (2.6 patches per 100 ha) to its 100th percentile (12.2 patches per 100 ha). The large effect of patch density at broad landscape extents (990-m focal landscapes) is consistent with past research that revealed that marten respond strongly to small amounts of forest fragmentation (Hargis and others 1999).

The area of a 990-m focal landscape occupied by non-stocked clear-cuts was the variable with the fifth largest effect size (Figure 16). Probability of marten occurrence

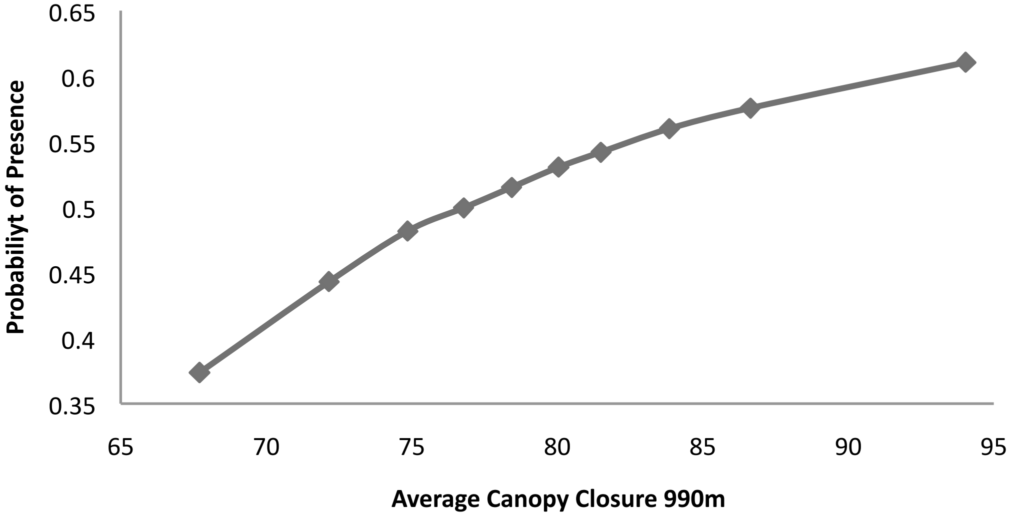


Figure 13. Change in probability of marten detection as the average canopy closure within a 990-m focal landscape increases from the 10th to the 100th percentile in the database, holding all other variables constant at their medians.

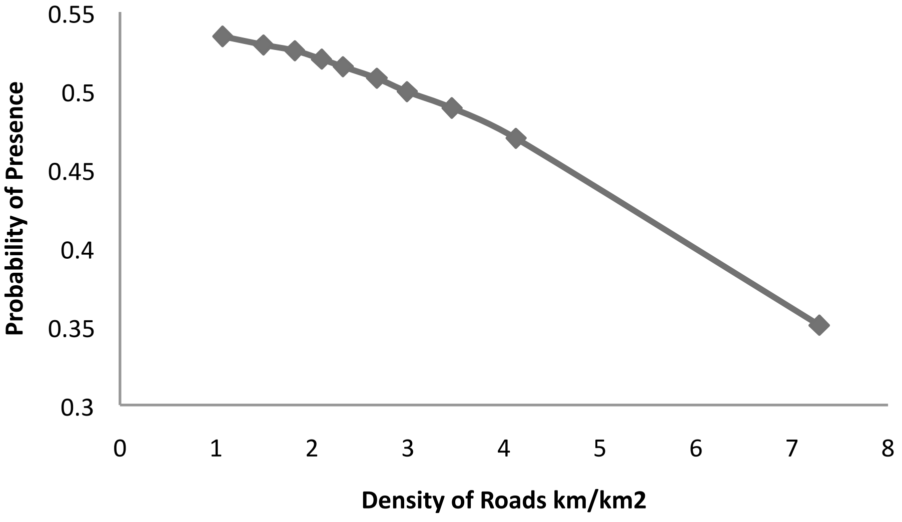


Figure 14. Change in probability of marten detection as the road density within a 1980-m focal landscape increases from the 10th to the 100th percentile in the database, holding all other variables constant at their medians.

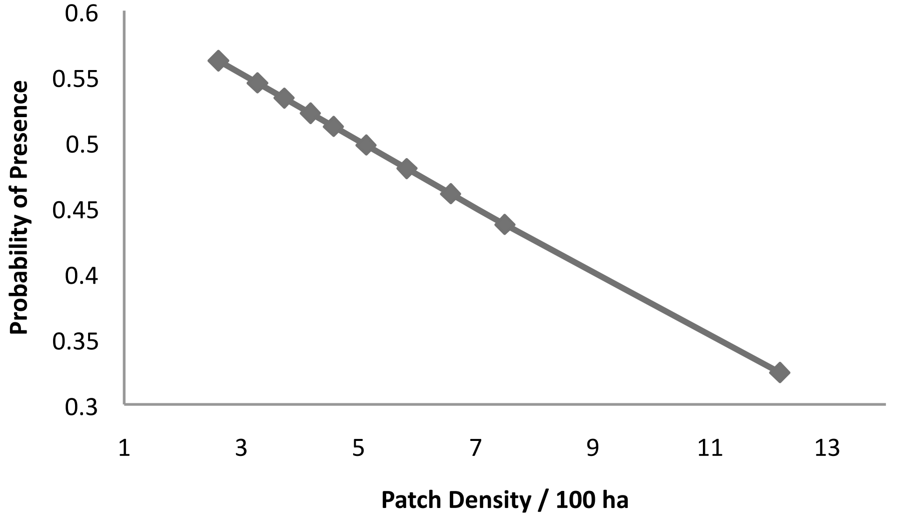


Figure 15. Change in probability of marten detection as density of patches of different seral stage within a 990-m focal landscape extent increases from the 10th to the 100th percentile in the database, holding all other variables constant at their medians.

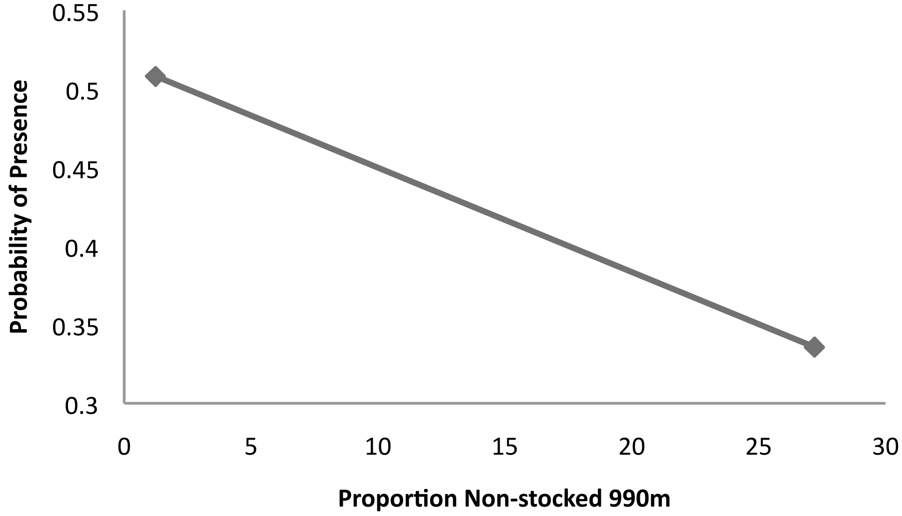


Figure 16. Change in probability of marten detection as the proportion of 990-m focal landscape occupied by non-stocked clear-cuts increases from the 10th to the 100th percentile in the database, holding all other variables constant at their medians.

decreased from 52% to 33% as the proportion of a 990-m focal landscape occupied by non-stocked clear-cuts increased from 2% (10th percentile) to 28% (100th percentile). This is consistent with previous research that showed that marten rarely used sites where more than 25% of forest cover was removed (Hargis and others 1999).

Elevation was tied with canopy cover as the variable with the highest AIC importance value (Table 4). However, it was the sixth of seven variables in terms of its effects size (Figure 17). Bivariate scaling identified a Gaussian function of elevation, with maximum suitability at 1400 m and a standard deviation of 400 m, as the most supported functional relationship between marten occurrence and elevation. The effects size calculation indicated that a change from the 10th (751 tm or 2051 m) to the 100th (1400 m) percentile of the transformed index increased probability of marten occurrence from 45% to 54%. This result indicates that while there is a very strong statistical relationship between elevation and marten occurrence (based on AIC variable importance), it has a relatively small effect size on actual probability of marten being present in comparison to the major landscape composition and configuration variables (canopy cover, western red cedar, road density, patch density, area non-stocked clear-cuts).

The percentage of a 90-m radius focal landscape consisting of large sawtimber was the least influential predictor variable, as judged by both AIC importance and effects size (Figure 18). However, local landscape area occupied by late seral forest was included in the final averaged model, indicating that marten detection was related to the area of a local 90-m focal landscape covered in late seral forest. A change from 0% to 100% of the focal landscape comprised of large sawtimber resulted in an increase in probability of occurrence from 48% to 55%. This indicates that American marten select for fine-scale foraging habitat within large size class, older forests. We can make this inference about foraging habitat due to the scale at which this variable entered the model; it was most highly significant at the finest scale tested (90 m), which corresponds to fine-scale behavioral choices within home ranges, and the hair-snare sampling method was built around marten foraging.

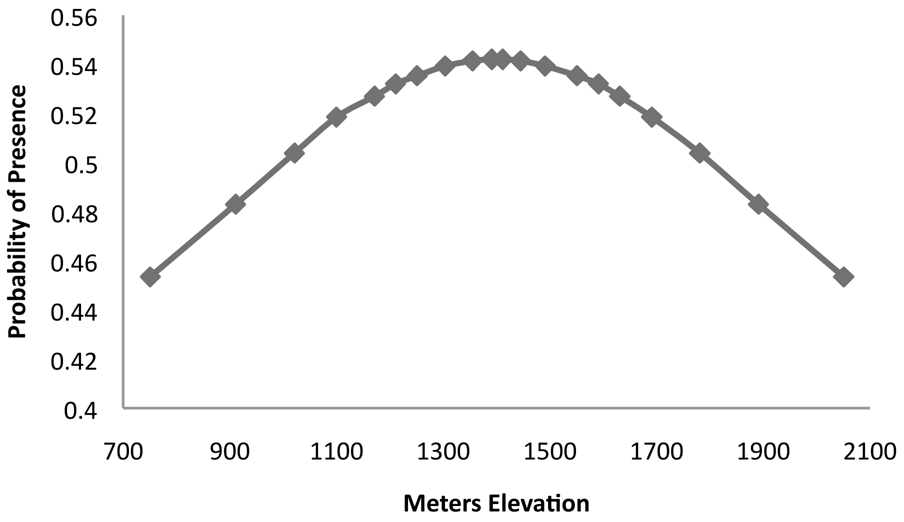


Figure 17. Change in probability of marten detection from the lowest to highest elevation in the study area, holding all other variables constant at their medians.

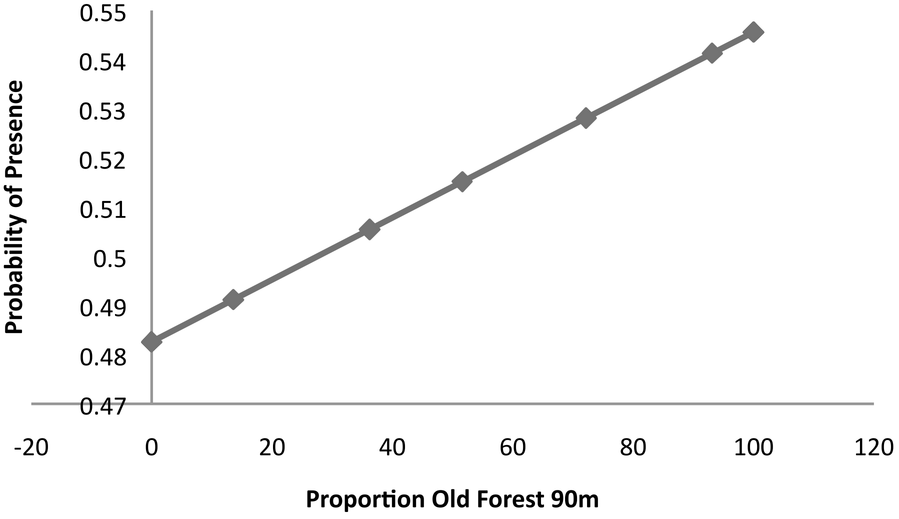


Figure 18. Change in probability of marten detection as proportion of late seral forest within a 90-m focal landscape extent increases from the 10th to the 100th percentile in the database, holding all other variables constant at their medians.

Management and Conservation Implications

The results of this study suggest that unfragmented, middle-elevation, mesic forest landscapes with high canopy closure are optimal habitat for American marten in northern Idaho. This is consistent with the results of previous studies, which have shown high sensitivity to landscape fragmentation and perforation by non-stocked clear-cuts (Hargis and others 1999), and strong preference of American marten in northern Idaho for mesic riparian forest conditions in unfragmented watersheds (Tomson 1999). However, this research has revealed several new insights that have substantial implications for conservation and management. The first is that marten select habitat at multiple spatial scales, selecting home ranges within unfragmented landscapes with high canopy closure and low road density; and those marten select foraging habitat within late seral, mesic, middle-elevation forests. This suggests that marten select home ranges largely based on the degree of fragmentation at broad landscape scales, which emphasizes the importance of maintaining large, unfragmented landscapes. Conversely, it suggests that local stand-level late seral forest conditions, while necessary, are insufficient to fully characterize habitat. Our results also suggest that perforations in the late seral matrix can have cumulative effects that extend much farther than the boundaries of disturbed patches. The results further suggest that late-seral forest types are important for fine-scale foraging behavior. This multiple-scale habitat selection emphasizes that critical habitat elements from both fine and broad scales are necessary to create suitable habitat for this species. For example, a patch of late-seral forest in a highly fragmented landscape with low canopy closure is not likely to be utilized. Conversely, a large, un-roaded landscape with high canopy closure is not likely to be highly utilized if it does not contain substantial areas of mesic, middle-elevation, late seral forest.

The second management implication relates to the importance of low fragmentation, middle-elevation forests. Our results show that middle-elevation forests with high biophysical suitability for western red cedar are particularly valuable as American marten habitat in northern Idaho. In the study area, most past timber harvest has occurred in lower and middle elevations, often concentrating on the most productive western red cedar cover types. Past timber management in northern Idaho may have been implemented in a way that disproportionately affected marten habitat quality, due to the: (1) pervasive road network, (2) dispersed clear-cutting in small patches, and (3) importance of middle-elevation cedar forest. In the post-World War II era, the U.S. Forest Service adopted a land management model based on regulated forests. The goal was to exert full control over harvest and wildfire across the land base. The first step in implementing a regulated forest was installation of an extensive road network. Roads were built throughout National Forest System lands, except for administratively withdrawn areas such as Wilderness or areas that were too topographically extreme for road construction. This resulted in a pervasive network of roads throughout the Forest. Our results show that road density has long-distance effects and can reduce habitat quality up to 2 km from a road. Given the highly extensive road network on National Forest lands in our study area, few areas are more than 2 km from a road, and road density in most parts of the study area is high enough to substantially affect marten habitat quality (Figure 14).

Second, timber harvest on National Forest System lands from the late 1950s until the 1990s was based on dispersing relatively small clear-cuts (10-20 ha) widely across the landscape. However, this style of management maximizes forest fragmentation and edge density (Wallin and others 1994). Forest fragmentation and perforation are among the largest negative impacts on marten habitat quality and occurrence (e.g., Hargis and others 1999). Our results confirmed this in northern Idaho, with large effects of the area of non-stocked clear cuts and density of forest patches with different seral stages at broad landscape extents. Cushman and McGarigal (2006) simulated a range of timber harvest patterns on the extent and pattern of American marten habitat and found that dispersed clear-cutting, similar to that previously implemented in northern Idaho on Forest Service lands, led to much faster and more severe loss of habitat quality for American marten than alternative cutting scenarios such as aggregated harvest blocks.

Third, past timber harvest in northern Idaho National Forest System lands was disproportionately concentrated in the high-productivity and highly valuable middle-elevation mesic forest types. These forest types provide the highest quality marten habitat; thus, harvest focused within these areas may have had more impact on marten populations than would be anticipated based on area harvested alone.

The fourth major management implication of our work is that the existence of late seral, middle-elevation, mesic forests is not a sufficient predictor of high-quality marten habitat. Specifically, our results indicate that marten are highly sensitive to road density and patch density at a broad landscape scale, suggesting that even if large portions of a landscape are composed of late seral, mesic forest, the quality of the landscape as marten habitat could be markedly reduced if the landscape is traversed by a relatively high density of roads or is perforated by a number of small patches with high-contrast edges. Importantly, our results also show that abandoned and decommissioned roads that do not appear on current travel maps still have substantial impact on marten habitat.

In combination, our findings suggest that marten habitat quality in northern Idaho may have been substantially reduced by timber harvest and road building in the past 100 years. This suggests that remaining roadless areas may be important source habitats for this species. Second, if marten conservation is a management objective, remaining late-seral, mesic forest types should be protected from harvest, some existing roads should be decommissioned and revegetated to reduce road densities, and additional roads should not be built in high-quality marten habitat.

Using Models to Assess and Monitor Habitat Conditions for American Marten

Generally speaking, most habitat models account for less than half the variation in species density or abundance (Morrison and others 2008). For example, Cushman and others (2008) empirically evaluated a suite of habitat models for multiple species and found that even dozens of habitat attributes from multiple spatial scales were unable to explain a majority of the variance in species abundances. Even when a model indicates strong associations between the probability of species occurrence and habitat gradients, it will usually fail to explain the majority of variability. In our case, even though our averaged model was highly statistically significant and performed moderately well discriminating presences from absences, it only explained approximately 15% of the variance in marten occurrence among sites. Therefore, the model predictions are not a surrogate for population estimation (Cushman and others 2008). However, models can be effective in evaluating the suitability of habitat for the species and the likely effects of past and potential future landscape change on habitat suitability. It is important for managers to understand the distinction between habitat suitability and actual population size.

For habitat monitoring to be useful as a guide for assessing population status, information on how habitat amounts or configurations can be linked with population viability or detection/non-detection is absolutely essential (Cushman and others 2011b). Adaptive management works by specifying resource goals, managing with the purpose to create or maintain these desired conditions, and monitoring results to confirm that the system is behaving as expected and that resources are moving toward the desired conditions (Cushman and McKelvey 2010). This approach presupposes that the state of the system is well known across time. The adaptive management paradigm sets high priority on developing ongoing analyses, based on monitoring, to continually adjust or change land management planning decisions and thereby efficiently move toward desired conditions (Cushman and McKelvey 2010). The adaptive management cycle involves: (1) a comprehensive evaluation of current resource conditions, (2) frequent monitoring and evaluation of conditions and trends relative to desired conditions, and (3) adaptation of management to improve performance in approaching or maintaining desired conditions. For this cycle to be effective, all three steps must be robust.

One way National Forest System managers evaluate current habitat conditions for emphasis species in light of past management actions is through cumulative effects analysis (CEA), a legal requirement under the National Environmental Policy Act (Schultz 2010). However, current CEA practice often fails to account for long-term or broad-scale impacts. Schultz (2010) identified insufficient monitoring and lack of formal thresholds and trigger points as a primary impediment to improving CEA. One way to improve assessment of habitat conditions of species of concern relative to desired conditions and to assess cumulative effects of past management is to integrate formal thresholds and trigger points with detailed and specific desired conditions statements (Cushman and others 2011c). It is critical to provide a formal declaration of desired conditions, how current conditions departure from desired conditions are quantified, and how management triggers are established to most efficiently move toward desired conditions.

In the context of our habitat model for American marten in northern Idaho, the model-averaged final logistic regression equation provides a means to predict habitat quality across the study area. Current habitat conditions on the analysis area can be mapped using this equation (e.g., Figure 11). Cumulative effects of past management activities, such as road building and logging, can be calculated by comparing the predicted habitat quality in the current landscape to that predicted in the analysis area prior to the specified management actions (e.g., Cushman and others 2006, 2011a). For use in adaptive management, a quantitative amount and configuration of quality habitat in the analysis area would be defined as an objective and specified as a desired condition. The model prediction of habitat quality would be the indicator used to quantify condition and trend relative to the objective. Quantitative triggers, expressed in terms of measured attributes, such as amount and configuration of quality habitat, would be established to identify when management actions would change. For adaptive management to be effective, practitioners must define their objectives and choose appropriate indicators and triggers up front and formally.

Future changes in habitat quality and pattern can be monitored over time by reapplying the habitat model to the analysis area after each management action or natural disturbance changes landscape composition and configuration (e.g., Cushman and others 2011b, 2011c). The area and configuration of high-quality marten habitat can then be compared with the quantitative and specific desired conditions statements that specify the desired range of quality marten habitat in terms of area, patch size, and patch isolation. Observing change away from desired conditions would trigger a change in management, while observing change toward desired conditions would not.

If a management change is indicated by surpassing a specified threshold in habitat area or fragmentation, the habitat model can provide useful guidance as to what changes are most likely to improve habitat condition effectively in relation to objectives. Specifically, the effects size graphs (Figures 12-16) provide a means to prioritize management actions that would have the biggest effects. For example, the model predicts that landscape-level canopy closure, road density, and forest perforation by clear cuts are all strong predictors of broad-scale patterns of marten occurrence. Mangers can use the graphs in Figures 12-16 to determine the expected effects of changing management to increase canopy closure, decrease road density, and/or reduce forest perforation by specific amounts. This information can guide a cost-benefit analysis of the management tradeoffs necessary to simultaneously meet multiple desired conditions objectives for multiple resources.

Simulation modeling can be particularly useful to guide managers in their evaluating alternative management strategies to achieve habitat desired conditions. For example, Cushman and others (2011a) used the habitat relationships model for American marten produced by Wasserman (2008) in conjunction with landscape dynamic simulation to evaluate the interaction among climate change, fire suppression, and vegetation harvest on the extent and quality of marten habitat in a watershed in western Montana. The analysis simulated landscape conditions under all combinations of a 2x2x2 factorial modeling experiment, which enabled formal quantification of the relative effects and interactions of climate change, fire suppression, and timber harvest on marten habitat. Importantly, by basing the analysis on an empirically developed statistical model, the analysis was able to quantitatively predict changes in the extent and pattern of quality habitat under each scenario, which provided the detailed and specific information managers need to evaluate alternative management scenarios.

Importance of Scale Optimization

For most species, biological information is available to guide decisions regarding appropriate variables for inclusion in candidate models, which greatly facilitates development of a suite of candidate models. However, the effect of a given variable on habitat selection may manifest itself at spatial scales ranging from a few meters to kilometers (e.g., Thompson and McGarigal 2002; Grand and others 2004). Most habitat selection studies fail to address this issue and simply evaluate alternative models that are based on predictor variables from a single, arbitrarily selected scale. Scientists have rarely evaluated the optimality of the scales at which they represent variables or the effect of incorrectly specifying scale (but see Thompson and McGarigal 2002; Grand and others 2004). The analysis presented here used a univariate optimization of variable scale in relation to marten occupancy, using the approach first published by Grand and others (2004). Shirk and others (in press) evaluated the sensitivity of habitat predictions in our northern Idaho study area to the scale of variables included. To test this, they compared a logistic regression model that was scale optimized, as in this paper, to a model that was constructed from a single scale of input variables. They chose a 90-m focal scale to represent the local patch character surrounding each detection station.

Shirk and Cushman (2011) found large differences in the scale at which habitat variables optimally predicted marten occurrence and the naïve scale of the original data set. There were also large differences between the scaled and unscaled models in terms of variable coefficients. Two variables (Percent Canopy Closure and Roads) changed signs between the scaled and unscaled forms of the model. This indicates an apparent reversal of relationship with marten occurrence as a function of scale, which has large implications for interpreting marten habitat selection. In addition, the magnitude of the coefficients changed dramatically for most of the other variables included in the model.

There was also substantial difference in predictive performance between the scaled and unscaled models from the Idaho study area. The scaled model had a substantially lower AICc value, higher percentage of observations correctly classified, and higher Kappa and AUC values. The scaling analysis also had a large impact on the apparent effects size of variables. Together, these results show that failure to optimize the scale at which each predictor variable relates to marten occurrence can have large effects on model performance and interpretation. Figure 19 shows the difference in predicted probability of occurrence between the scaled and unscaled models. The scaled model predicts substantially higher probability of occurrence than the unscaled model in middle-elevation, mesic forested landscapes with low road density, while the unscaled map over-predicts probability of marten occurrence in less optimal situations, such as in low-elevation, non-forested sites. The unscaled model is much weaker and provides substantially different predictions, which would lead to dramatically different interpretations in relation to what factors are important as components of marten habitat and at what spatial scale marten most strongly select them.

Differences Between Habitat Quality and Habitat Connectivity

We found that marten occurrence in this study area is highly dependent on high canopy cover, low forest fragmentation, and low road density at broad spatial scales. This sensitivity to forest fragmentation and mesic, middle-elevation forest is highly consistent with the preponderance of past studies of American marten habitat associations (Buskirk and Powell 1994; Ruggiero and others 1994; Hargis 1996; Bissonette and others 1997; Chapin and others 1998; Hargis and others 1999; Tomson and others 1999). However, Wasserman and others (2010) found that genetic distances were not independently related to any of these factors, indicating that habitat selection and gene flow of American marten may be driven by different factors at different scales. This may not be surprising, as habitat selection reflects the behavior of individual organisms to maximize fitness within home ranges, while gene flow is driven by mating and dispersal events. These are functionally and biologically different processes. Habitat suitability may not be a reliable proxy for predicting landscape effects on gene flow. This highlights the importance of not assuming that a known habitat relationship optimally reflects the landscape features governing gene flow.

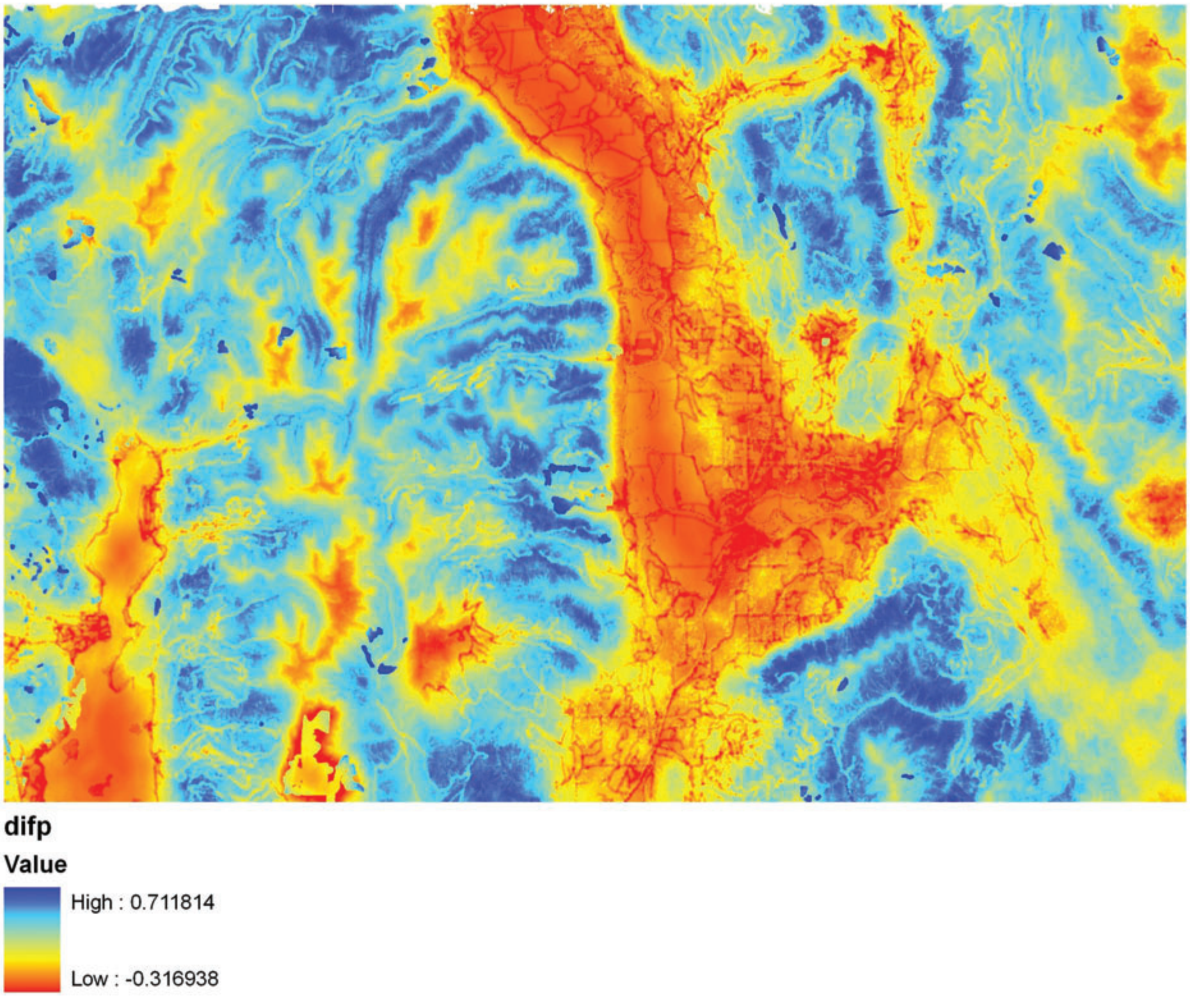


Figure 19. Difference in predicted probability of presence between the optimized scaled model in this paper and a single-scale model from Shirk and others (2011). The areas in blue are predicted to have higher probability of marten occurrence in the scaled model than the unscaled model, while areas in red are predicted to have higher probability of marten occurrence in the unscaled model than the scaled model. The scaled model predicted higher probability of occurrence in high-quality habitat and lower probability of occurrence in low-quality habitat than did the unscaled model.

Conclusions

We explored the scale dependency of habitat relationships of American marten in northern Idaho and found dramatic differences in the apparent nature and strength of relationships between marten occurrence and a number of habitat variables across a range of spatial scales. These differences include reversals in the direction of an observed association from positive to negative and frequent dramatic changes in the apparent importance of a habitat variable as a predictor of marten occurrence. Logistic regression on the optimally scaled input variables suggests that at the scale of home ranges, marten select landscapes with high average canopy closure and low fragmentation. Within these low-fragmentation landscapes, marten select foraging habitat at a fine scale within late-seral, middle-elevation mesic forests. In northern Idaho, optimum American marten habitat, therefore, consists of landscapes with low road density and low density of non-forest patches with high canopy closure and large areas of middle-elevation, late successional mesic forest. Comparison of current landscape conditions to those expected under the historic range of variability indicated that road building and timber harvest in the past century may have substantially reduced the amount of suitable marten habitat in northern Idaho. Our results are generally consistent with previous research in the Rocky Mountains, with additional insights related to the relative importance, functional form, and scale at which each habitat variable has the largest influence on marten occurrence.

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