



Research Article

Evaluating Habitat Suitability Models for Nesting White-Headed Woodpeckers in Unburned Forest

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ABSTRACT Habitat suitability models can provide guidelines for species conservation by predicting where species of interest are likely to occur. Presence-only models are widely used but typically provide only relative indices of habitat suitability (HSIs), necessitating rigorous evaluation often using independently collected presence-absence data. We refined and evaluated presence-only habitat suitability models for nesting white-headed woodpeckers (*Picoides albolarvatus*), a narrowly distributed species of conservation concern that occupies dry conifer forests of the Inland Pacific Northwest, USA. We developed 2 models using Mahalanobis D^2 and Maxent techniques from nest location datasets collected on the eastside of the Cascade Mountain Range, Oregon (1 dataset in 1997–2004 and another, sampling a broader spatial extent, in 2010–2011). Consistent with known ecology of white-headed woodpeckers, both HSI models related positively with percent ponderosa pine, moderate levels of canopy cover (approx. 40%), and moderate-to-high levels of heterogeneity in forest structure. Unlike Mahalanobis HSIs, however, Maxent HSIs were consistently and positively related with nest prevalence and positively related with habitat use estimated with independent point count data. Locations with high Maxent HSIs were characterized by canopy openings adjacent to closed canopy forests. The fact that this habitat feature was described by Maxent HSIs but not by Mahalanobis HSIs possibly explains why Maxent HSIs better predicted white-headed woodpecker occurrence. Additionally, we used presence-absence data for model evaluation that sampled a broader spatial extent than nest surveys and therefore allowed us to demonstrate the generality of Maxent HSIs. Additional nest location data collected across a broader portion of the species range would be valuable for further model improvement and evaluation, but until such data are available, we recommend use of Maxent HSIs to guide habitat conservation and restoration efforts in unburned dry forests of Oregon. Published 2014. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS forest restoration, Mahalanobis D^2 , Maxent, model validation, *Picoides albolarvatus*, presence-only models, species distributions.

The white-headed woodpecker (*Picoides albolarvatus*) is a species endemic to dry, conifer forests of western North America (Garrett et al. 1996), and habitat for this species has been a focus of forest restoration (Hessburg et al. 2005). Breeding habitat consists of mature forest landscapes containing canopy openings and large-coned pine trees (e.g., *Pinus ponderosa*) that produce seeds, an important food resource (Ligon 1973, Raphael and White 1984, Garrett et al. 1996). Nest placement frequently occurs in open-canopied forest patches often adjacent to relatively closed-canopy forest thought to provide critical food resources (Wightman et al. 2010, Hollenbeck et al. 2011). These complex habitat requirements make identification of suitable breeding habitat challenging.

Habitat suitability index (HSI) models are used to guide land management decisions aimed at species conservation (Maiorano et al. 2006, Barrows et al. 2008, Keenan et al. 2011). Habitat suitability models identify statistical relationships between species and their environments. These models can be used to predict the environments and geographic locations where species are most likely to occur. Models typically provide continuous indices of habitat suitability (HSI; 0–1 range) that indicate likelihood of species occurrence (0 = least likely, 1 = most likely) and can be discretized into classes that discriminate high- from low-suitability habitat (Hirzel et al. 2006, Freeman and Moisen 2008, Liu et al. 2013).

Habitat suitability models use different types of data to derive metrics with different meanings (Lele et al. 2013). Presence-absence models estimate an HSI that portrays the probability of species presence at specific locations within a specified timeframe (e.g., occupancy probabilities; MacKenzie et al. 2002, 2006), requiring both habitat use (species presence) and

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non-use (absence) data. Habitat suitability models derived from resource selection theory aim to quantify habitat selection by comparing used locations to a random sample representing locations available to the species (HSI = probability of selecting a location over other available locations; e.g., Phillips et al. 2006, McDonald 2013). Presence-only habitat suitability models quantify the environmental distribution of used locations (habitat-use distribution), requiring only a representative sample of habitat measurements at used locations (e.g., for distance models, HSI = similarity to used habitat; Rotenberry et al. 2006).

Habitat suitability indices generated by different types of models are related (Lele et al. 2013). Outputs from all aforementioned models are largely the realization of habitat selection applied across a particular set of available habitats. Habitat suitability indices typically attempt to infer species distributions from environmental relationships with occurrence data. Thus, if different types of HSIs are fitted to data sampling the same population within the same environmental range, outputs should be correlated. However, occurrence data collected over a limited range of environments and geographic variation in environmental relationships may limit the ability of HSI models to provide generally accurate predictions (Thuiller et al. 2004, Morrison 2012). Additionally, because models quantify environmental relationships differently, their HSIs may diverge when applied in novel environments (Heikkinen et al. 2012, Latif et al. 2013).

Evaluation of HSI models with multiple criteria and independent datasets is invaluable for verifying their utility for guiding management. Evaluation with independent data is standard practice to verify model predictive capacity. Most often, a randomly selected subset of data are withheld from model development for subsequent evaluation (Guisan and Zimmermann 2000). However, to fully evaluate their predictive value, models should also be tested against independently collected data that preferably sample beyond the geographic extent of model development (Heikkinen et al. 2012, Wenger and Olden 2012, Bahn and McGill 2013).

We continued the process of developing and evaluating habitat suitability models for nesting white-headed woodpeckers in unburned forests. Hollenbeck et al. (2011) developed an HSI model that quantified the environmental distribution of white-headed woodpecker nest sites in the East Cascade Mountains using the partitioned Mahalanobis D^2 technique (Rotenberry et al. 2006). When we applied the Hollenbeck et al. (2011) model outside the originally sampled geographic extent, the model assigned relatively low HSI values to new nest locations, suggesting a lack of generality. Therefore, we used the original and new nest locations to develop new habitat suitability models using 2 modeling techniques: Mahalanobis D^2 and Maxent. Mahalanobis HSIs quantify habitat-use distributions, whereas Maxent HSIs quantify habitat selection, but both can be used to infer species geographic distributions (Phillips et al. 2006, Rotenberry et al. 2006). We evaluated the new models using nest locations withheld from model development and independently collected presence-absence data generated

from point count surveys. We evaluated both continuous HSIs and suitability classifications derived from HSI thresholds using nest location and point count data.

STUDY AREA

For model development, our study area included forests in the East Cascade and Blue Mountains of eastern Oregon, USA. Nests were located in the Sisters Ranger District on the Deschutes National Forest (44°17' N, 121°33' W) and the Chemult and Chiloquin Ranger Districts on the Fremont-Winema National Forest (43°13' N, 121°47' W and 42°34' N, 121°53' W, respectively), on the eastern slope of the Cascade Mountain Range (Fig. 1). Forests were characterized as dry, mixed conifer and were dominated by ponderosa pine (*Pinus ponderosa*), lodgepole pine (*P. contorta*), or a mix of conifer species typically including Douglas-fir (*Pseudotsuga menziesii*; for additional details, see Hollenbeck et al. 2011). Prior to Euro-American settlement, dry mixed conifer forests of the Inland Northwest were burned by frequent (1–25 years) low- or mixed-severity fires (<20% or 20–70% tree mortality, respectively; Hessburg et al. 2005). Extant dry forest landscapes support primarily mixed and high-severity fires, and these fires are occurring over much larger areas than was formerly the case (Hessburg et al. 2005).

We conducted point count surveys used for model evaluation across a broader geographic extent that included portions of the East Cascade and Blue mountain ranges (Fig. 1). Although the 2 mountain ranges occur in different ecoregions (East Cascade Mountain Range in the East Cascade-Modoc Plateau Ecoregion, and the Blue Mountains in the Middle Rockies and Blue Mountains ecoregions; Baily 1995), both have similar historical disturbance regimes (Hessburg et al. 2005, Franklin and Johnson 2012).

METHODS

Field Surveys

We initially located nests in May–June 1997–2004, in the Deschutes and Fremont-Winema National Forests (Fig. 1). We systematically searched for nest cavities following standard protocol during the nesting season (Dudley and Saab 2003, Hollenbeck et al. 2011). We included cavities only where nesting activity was confirmed. Active nests contained eggs or young, or were identified based on adult behavior indicative of food delivery, frequent visits, or extended time spent in the cavities (Dudley and Saab 2003). We visually inspected cavity contents using a telescoping camera (TreeTop II System, Sandpiper Technologies, Inc., Manteca, CA).

In May–June 2010–2011, we located more nests across a broader geographic extent within each National Forest (Fig. 1). We implemented our nest searching protocol in areas surrounding 37 2.7-km transects randomly located in forests dominated or co-dominated by ponderosa pine in the Sisters and Chemult-Chiloquin Ranger Districts. Ponderosa pine dominance was based on output from gradient nearest neighbor (GNN) analyses (Ohmann and Gregory 2002).

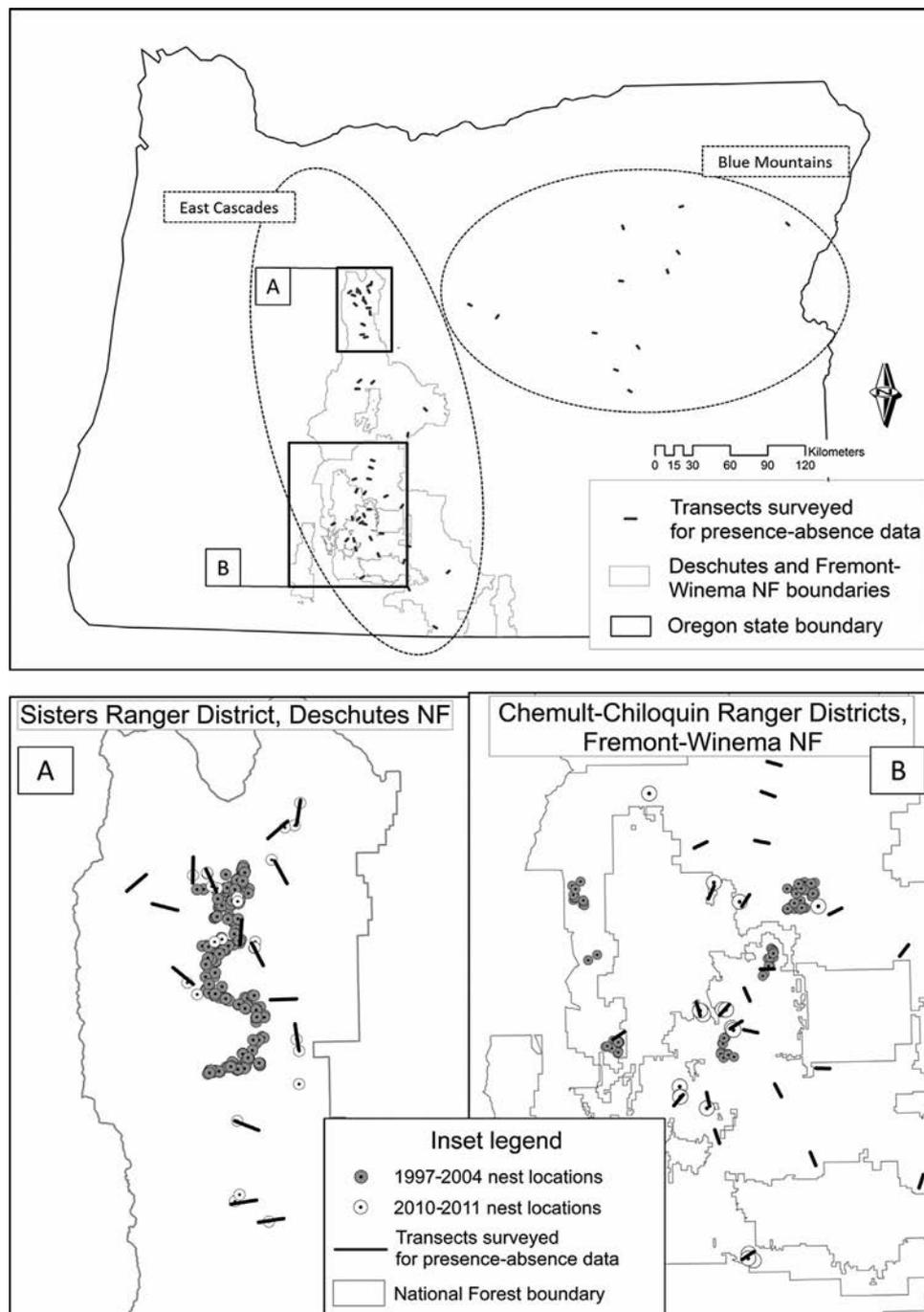


Figure 1. Study area for development and evaluation of white-headed woodpecker habitat suitability models. Nest and transect locations on the A) Sisters, and B) Chemult-Chilouin Ranger Districts, United States Department of Agriculture National Forest system.

When nest searching along transects, we searched within 400 m of the transect centerline, although surveyors sometimes followed birds thought to be nesting ≤ 2 km away.

We conducted point count surveys in 2010–2012 along 58 2.7-km transects randomly located in forests dominated or co-dominated by ponderosa pine. Transects were spaced ≥ 1 km apart and we field verified the status of ponderosa pine. We established 10 points spaced roughly 300 m apart along each transect. During each point visit, surveyors broadcast 20 seconds of white-headed woodpecker calls and

drumming followed by 30 seconds of silence; we repeated this pattern 3 times in 3 directions (120° separation). At the end of the last broadcast, surveyors would listen for 2 additional minutes (4.5 min total). If the surveyor detected a white-headed woodpecker, they immediately ended the survey. Surveyors estimated that individuals were rarely detected >150 m from survey points. We surveyed 13 transects in the Sisters Ranger District (Deschutes NF) 3–4 times each (mean = 3.77, SD = 0.80) in 2010 (10 May–1 Jul), 46 transects throughout the East Cascade and Blue

mountains (including 1 of the 13 Sisters transects) approximately twice each (mean = 2.04 visits, SD = 0.31) in 2011 (26 Apr–5 Jul), and 25 transects (12 Blue Mountain and 13 East Cascade transects) twice each in 2011 (1 May–26 Jun). Thus, we surveyed 33 transects in only 1 year (2010 or 2011), 24 transects in 2 years (2011–2012), and 1 transect in the Sisters Ranger District during all 3 years (2010–2012).

Environmental Data

We compiled environmental variables describing topography and forest structure from remotely sensed data at a 30-m resolution (Table 1). We derived topographic variables from digital elevation model (DEM) layers (United States Geological Survey 2012) and forest structure variables from GNN data (Ohmann and Gregory 2002). We assumed pixels classified as non-forest by GNN to have 0% canopy cover. We summarized variables at 3 scales, the individual pixel containing the nest or point (0.09 ha; slope, cosine aspect), 0.81 ha surrounding the nest or point (local-scale canopy cover), and 314 ha surrounding the nest or point (landscape-scale canopy cover, percent ponderosa pine, edge density; Table 1). We used percent of ponderosa pine forest in a 314-ha area surrounding the nest or point rather than elevation (see Hollenbeck et al. 2011) because ponderosa pine dominance is related to elevation and more directly relevant to white-headed woodpecker ecology. Previous white-headed woodpecker models used interspersed-juxtaposition (IJI) to quantify mosaics of open- and closed-canopy forests (Wightman et al. 2010, Hollenbeck et al. 2011). We instead used edge density because IJI cannot be calculated for neighborhoods with <3 patch types (McGarigal and Ene 2013). We used GNN variables derived from Landsat imagery recorded in 2000 and 2012 for 1997–2004 and 2010–2012 nest locations and point count data, respectively.

Model Development

We developed HSI models using 2 techniques: partitioned Mahalanobis D^2 (HSI_{Mahal}; Rotenberry et al. 2006) and Maxent (HSI_{Max}; Phillips et al. 2006). Both techniques have

proven successful at discriminating used from unused locations for a variety of species when evaluated with independent presence-absence data (Elith et al. 2006, Tsoar et al. 2007). Nevertheless, model outputs can be highly sensitive to changes in spatial extent (Latif et al. 2013). We acknowledge that the original (1997–2004) and new (2010–2012) white-headed woodpecker data represented partially overlapping spatial extents, different sample sizes, and were collected using different sampling designs (Table 2). To reduce potential biases related to sampling design, we accounted for potential biases related to roads, sampling distribution, and sample size during model development and evaluation (Appendices S1–S3, available online at www.onlinelibrary.wiley.com). We used pixels containing >1 nest only once for modeling (404 nests were located within 376 pixels used for modeling). We plotted pixel HSI values (mean ± 1 SD) for each nest or point against environmental variables for 10,000 available pixels (for description, see Appendix S1) to identify habitat relationships (i.e., dose-response plots; Hanser et al. 2011).

Mahalanobis D^2 model.—Mahalanobis D^2 model HSI (HSI_{Mahal} scores) portray standardized environmental distances (re-scaled 0–1) from the multivariate mean for species presence locations (Appendix S2; Rotenberry et al. 2006). We constructed HSI_{Mahal} models using 2–6 variables consisting of percent ponderosa pine, edge density, and every combination of the remaining 4 variables (Table 1; for their importance to white-headed woodpeckers, see Wightman et al. 2010, Hollenbeck et al. 2011). Variance partitioning can improve model performance and parsimony (Rotenberry et al. 2006, Preston et al. 2008) but not in this study, so we present only unpartitioned HSI_{Mahal} models (i.e., those representing 100% of the variation described by each variable combination; Appendix S2). We selected the most parsimonious model (fewest variables) that achieved relatively high median nest HSI_{Mahal} for further evaluation. We calculated median nest HSI_{Mahal} scores for evaluation data withheld from model development (Appendix S2).

Maxent model.—Maxent models describe environmental distributions of species-use locations in terms of their differences from available locations (Phillips et al. 2006, Elith et al. 2011, Merow et al. 2013). Based on these differences, HSI_{Max} models estimate a relative probability of habitat selection. We fitted models to subsamples of nest location and availability data for which we adjusted sample

Table 1. Variables used for development of Maxent and Mahalanobis D^2 models of habitat suitability for nesting white-headed woodpeckers, eastern Oregon, USA.

Variable name ^a	Description
Slope	Pixel slope as % rise over run
Cosine aspect	Pixel cosine-transformed orientation of slope (unitless)
Local-scale canopy cover	Percent canopy cover for 0.81-ha (3 × 3 cell) neighborhood
Landscape-scale canopy cover ^b	Percent canopy cover for 314-ha (1-km radius) neighborhood
Ponderosa pine ^b	Percent ponderosa-pine-dominated forest for 314 ha (1-km-radius) neighborhood
Edge density ^b	Length of edge between alternate patch types characterized according to canopy cover class (10–40% and 40–80%) within 314-ha (1-km radius) neighborhood.

^a Variables derived from 30-m resolution land cover data collected in 2002 and 2012.

^b 314-ha (1-km radius) neighborhoods approximated home range sizes for white-headed woodpeckers reviewed by Garret et al. (1996).

Table 2. Number of 30-m pixels (*n*) containing a nest and median nest habitat suitability index (HSI) scores (25th, 75th percentiles) from habitat suitability models for nesting white-headed woodpeckers in the Deschutes and Fremont-Winema National Forests, Oregon. Median scores are for original (1997–2004; Hollenbeck et al. 2011) and newly collected (2010–2011; this study) nest locations.

	1997–2004	2010–2011
<i>n</i>	340	36
Original model		
Mahalanobis	0.58 (0.27, 0.81)	0.36 (0.01, 0.60)
New models		
Mahalanobis	0.59 (0.36, 0.74)	0.61 (0.21, 0.87)
Maxent	0.47 (0.39, 0.55)	0.51 (0.45, 0.56)

sizes to balance fit across data subsets representing different time periods (Kramer-Schadt et al. 2013; Appendix S3). For HSI_{Max} , analysts are advised to favor simple models that perform comparably to more complex models to facilitate understanding of habitat relationships (Merow et al. 2013). We therefore developed HSI_{Max} models for only linear and quadratic relationships with the 6 habitat variables (Table 1). We verified that the simpler HSI_{Max} performed comparably to the most complex (fully parameterized) model.

Model Evaluation

Evaluation with nest location data.—We compared the original Hollenbeck et al. (2011) model to HSI_{Mahal} and HSI_{Max} models by comparing medians and quartiles (25th and 75th percentiles) for the corresponding HSI values assigned to nests from our 2 time periods (Table 2). Because others evaluate HSI_{Mahal} models based on the consistency of HSI_{Mahal} values assigned to used locations (Preston et al. 2008), we looked for greater consistency of nest HSIs across time periods as a sign of improvement over the Hollenbeck et al. (2011) model.

We further evaluated HSI_{Mahal} and HSI_{Max} models and HSI thresholds for classifying suitable habitat using performance metrics calculated with nest location data. We calculated sensitivity (the proportion of nest pixels correctly classified as high-suitability) and specificity (proportion of available pixels classified low-suitability) to evaluate HSI classification thresholds (Jiménez-Valverde et al. 2013). Sensitivity and specificity for alternate thresholds were calculated using nest locations withheld from model development (Appendices S2, S3). We identified thresholds that maximized predictive gain ($PG = \text{sensitivity} - [1 - \text{specificity}]$; Browning et al. 2005), which also maximizes the sum of sensitivity and specificity (Liu et al. 2013). Using maximum PG thresholds, we categorized moderate-to-high-suitability habitat ($HSIs > \text{threshold}$; hereafter high-suitability habitat) or unsuitable-to-low-suitability habitat ($HSIs < \text{threshold}$; hereafter low-suitability habitat). Additionally, we evaluated several HSI thresholds at intervals of 0.05 above and below maximum PG thresholds to provide additional options for managers with varying goals.

In addition to threshold-based evaluation, we generated calibration plots to examine the extent to which nest prevalence (ratio of nest to available pixels) consistently increased with increasing HSI scores (Phillips and Elith 2010). We generated calibration plots using a dataset of nest and available pixels sampled following the same steps used to develop the HSI_{Max} model (Appendix S3).

Evaluation with point count data.—We used point count data and occupancy models to further evaluate our HSI models. We related the probability of white-headed woodpecker occupancy during the study period, adjusted for detection probability to HSI_{Mahal} and HSI_{Max} scores. We assumed that white-headed woodpeckers during the breeding season were more likely to occur and be detected at survey points within suitable nesting habitat. We used hierarchical occupancy models fitted within a Bayesian

framework to estimate probability of occupancy for each survey point ($n = 580$; Royle and Kery 2007). This probability of a point being occupied was modeled as a function of maximum HSI_{Mahal} or HSI_{Max} values within 150 m of the survey point (the maximum distance of most detected birds) as covariates. We used static occupancy models for which repeat surveys of points throughout the study period informed estimation of detection probabilities (MacKenzie et al. 2002).

Probability of occupancy is modeled on a logit scale, so we used alternately scaled versions of HSI_{Mahal} and HSI_{Max} as continuous covariates (Appendix S4). Additionally, we used our HSI classification thresholds to generate categorical covariates to determine if probability of occupancy differed between high-suitability (1) and low-suitability (0) survey points. We used Bayesian P -values to assess the statistical support for HSI relationships with probability of occupancy ($P = \text{proportion posterior samples of } \beta_{HSI} \leq 0$), whereby low P -values indicate statistical support for a positive relationship. All occupancy models included a random effect to account for variation in probability of occupancy among transects ($n = 58$; see also Royle and Kery 2007). All models also included a quadratic fixed effect of survey date and a random year effect as covariates of detection. We fitted occupancy models using JAGS (v. 3.3.0; Plummer 2003) accessed from R (v. 3.0.1; R Core Team 2013) via the R2jags package (Su and Yajima 2014). Additional details and rationale for occupancy models are provided in Appendix S4.

RESULTS

Areas used for nest searching and point count surveys were generally similar with respect to our 6 habitat variables (Table 3). Sites tended to have moderate slopes (9–12%) and comparable levels of canopy cover at the local and landscape scales (43–45%). Sites were consistently dominated by ponderosa pine (70–72%) and contained 64–68 m/ha of edge between open- and closed-canopy patches. Our data also indicated that most sites were on eastern aspects. Nests tended to occur in pixels with less slope, more north-facing aspect, less local-scale canopy cover, more ponderosa pine, and more edge than available sites (Table 3).

Nest Site HSI Comparison

HSI_{Mahal} .—Median nest HSI_{Mahal} values ranged from 0.463 to 0.581 across the 15 candidate models. Median nest HSI_{Mahal} values were highest for 4 models (0.56–0.58), of which we selected the most parsimonious (Table 4). The selected model included landscape-scale canopy cover, percent ponderosa pine, and edge density. The HSI_{Mahal} values were highest for pixels with moderate (25–50%) landscape-scale canopy cover, high percentage of ponderosa pine (>75%), and relatively high amounts of edge (>75 m/ha; Fig. 2).

HSI_{Max} .—The HSI_{Max} model that allowed only linear and quadratic relationships performed comparably to the model that allowed all possible relationships (Appendix S3). The most informative predictors in the simpler HSI_{Max} (selected for further evaluation) were percentage of ponderosa pine,

Table 3. Descriptive statistics (mean [SD]) for habitat variables at white-headed woodpecker nest locations (30-m pixels containing nests), at available locations (pixels sampled from the landscape within which nests were located), and points used for call-broadcast surveys. We drew half ($n = 5,000$) of available locations from areas where original nests (1997–2004) were located, and the remaining half from areas where new nests (2010–2011) were located.

Variable	Nest locations ($n = 376$)	Available locations ($n = 10,000$)	Survey points ($n = 580$)
Slope (%)	7.6 (8.0)	8.9 (10.2)	12.3 (11.0)
Cosine aspect	0.07 (0.66)	0.02 (0.66)	-0.14 (0.66)
Local-scale canopy cover (%)	40.1 (13.1)	43.1 (14.1)	44.6 (15)
Landscape-scale canopy cover (%)	43.2 (7.5)	43 (9.5)	44.5 (11.1)
Percent ponderosa pine	79.9 (15.0)	72 (19.4)	70.2 (18.4)
Edge density (m/ha)	73.4 (25.2)	67.5 (28.7)	64.1 (31.7)

and local- and landscape-scale canopy cover (Fig. 3). This model assigned higher HSIs to pixels as the percentage of ponderosa pine increased, at low to moderate levels (<40%) of local-scale canopy cover, and at moderate levels (25–50%) of landscape-scale canopy cover (Fig. 3).

Increasing percent ponderosa pine and moderate levels of canopy cover were consistently identified as high suitability white-headed woodpecker nesting habitat by both HSI_{Mahal} and HSI_{Max} models (Figs. 2 and 3). Habitat suitability indices were not related to slope or aspect. Both models assigned relatively low HSIs to areas with high local-scale canopy cover and low edge density. The models diverged at high edge densities, with HSI_{Max} suggesting that nesting habitat suitability increases, whereas HSI_{Mahal} indicated suitability declined. Additionally, at relatively low levels of local-scale canopy cover, HSI_{Max} values remained stable, whereas HSI_{Mahal} values declined.

Model Comparison and Evaluation

Nest location data.—Median nest HSI_{Mahal} and HSI_{Max} scores were more similar across datasets than median scores calculated from the original Hollenbeck et al. (2011) model (Table 2), indicating HSIs from our newer models were more general. At optimal (max. PG) thresholds (i.e., $HSI_{Mahal} = 0.31$, $HSI_{Max} = 0.46$) and some alternative thresholds, both models classified a majority of nest pixels (>60%) as high-suitability (Table 5) while also classifying a substantial portion of the landscape as low-suitability (specificity = 0.28–0.56 for thresholds with sensitivity >0.60; Table 5). The HSI_{Max} model was more informative than the HSI_{Mahal} model, however (predictive gain = 0.17 and 0.09 for optimal HSI_{Max} and HSI_{Mahal} thresholds, respectively). Additionally, nest prevalence was more clearly positively related with HSI_{Max} compared to HSI_{Mahal} scores (Fig. 4).

Point count data.—We detected white-headed woodpeckers during 144 of 1,950 survey visits at 111 of 580 points along 39 of 58 transects. Survey points were associated with a wide range of HSI values (mean [SD, min.–max.] $HSI_{Mahal} = 0.55$ [0.12, 0.11–0.84]; $HSI_{Max} = 0.44$ [0.32, 0.00–1.00]). The HSI_{Mahal} outputs at point count locations were not related to probability of the site being occupied from the occupancy models (Fig. 5A). In contrast, we found a statistically supported positive relationship between HSI_{Max} and probability of point count location being occupied (Fig. 5B). Three HSI_{Max} thresholds were significantly related to probability of occupancy, whereas relationships were not supported for any HSI_{Mahal} thresholds (Table 5). Occupancy models used to estimate these relationships provided a reasonable fit to the data and accounted for inter-annual and intra-seasonal variation in detectability, as well as variation among transects (Appendices S4, S5).

DISCUSSION

Habitat suitability models can serve as useful tools for predicting the distribution of white-headed woodpeckers during the nesting season. In particular, our HSI_{Max} model appeared to outperform the HSI_{Mahal} model in differentiating nest from available locations and predicting white-headed woodpecker occupancy of point count locations. Both HSI_{Mahal} and HSI_{Max} models characterized locations used and selected for nesting more generally than did the Hollenbeck et al. (2011) model. Nevertheless, HSI_{Max} scores were better able to distinguish nest from available locations. Only HSI_{Max} was clearly positively related to nest prevalence as indicated by calibration plots and significantly positively related with probability of white-headed woodpecker occupancy of a site estimated with independent data from point count surveys. Several HSI_{Max} thresholds were also

Table 4. Variables and median nest habitat suitability index values (HSI_{Mahal}) for selected and alternative Mahalanobis D^2 models for nesting white-headed woodpeckers in eastern Oregon, 1997–2004 and 2010–2011. Means and standard deviations for median nest HSI_{Mahal} are for 500 evaluation datasets withheld from model development. Variables included in each model are indicated with an x.

Slope	Cosine aspect	Local canopy cover	Landscape canopy cover	Ponderosa pine (%)	Edge density	Median nest HSI_{Mahal} (SD)
Selected model						
			x	x	x	0.562 (0.147)
Other highest median nest HSI_{Mahal} models						
x			x	x	x	0.581 (0.151)
		x	x	x	x	0.562 (0.16)
x		x	x	x	x	0.559 (0.17)
x	x		x	x	x	0.539 (0.162)
		x		x	x	0.537 (0.14)

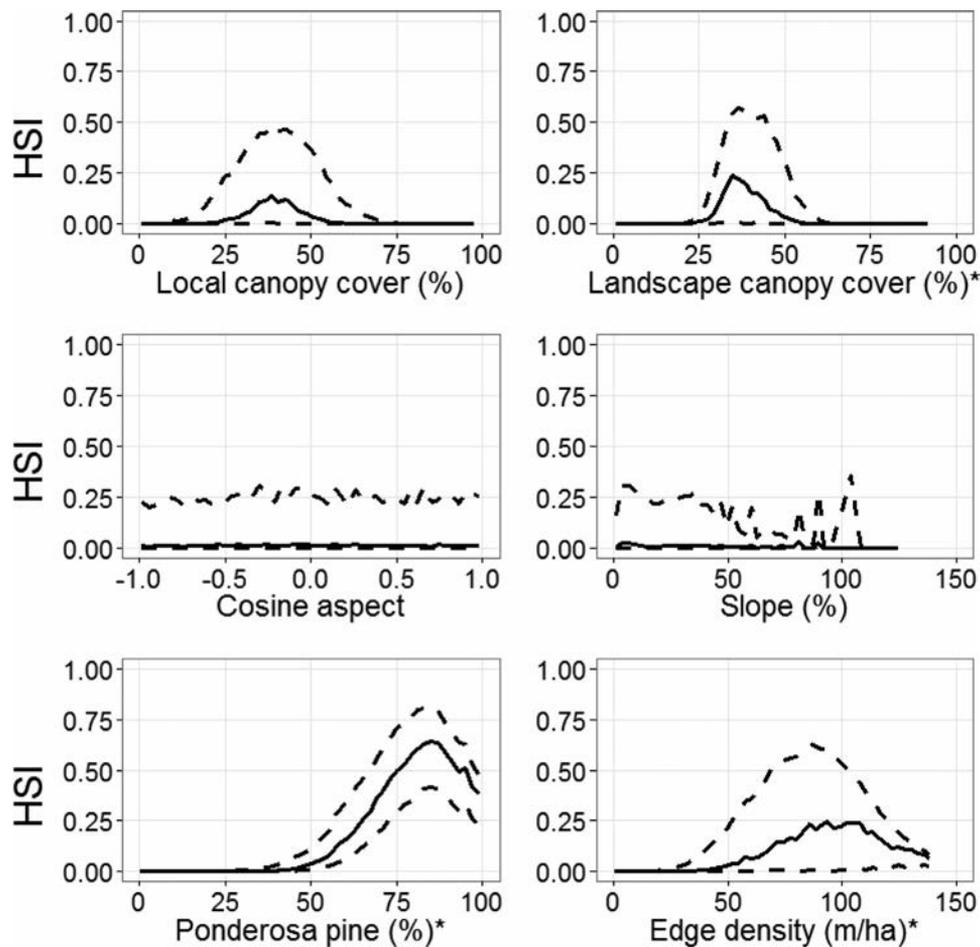


Figure 2. Mahalanobis D^2 model mean (solid line) \pm standard deviation (dashed lines) habitat suitability index (HSI) values for nesting white-headed woodpeckers by environmental variables measured in eastern Oregon, 2002 and 2012. Asterisks indicate variables that were included in the final selected model.

significantly related to white-headed woodpecker occupancy of point count locations. Therefore, the HSI_{Max} model appears better suited to inform the presence of white-headed woodpecker habitat for management in unburned forests of eastern Oregon.

Differences in model performance and habitat relationships emphasized between HSI_{Max} and HSI_{Mahal} models were possibly attributable to how the models quantified environmental relationships with nest locations. Heterogeneity in canopy cover is a key element of suitable nesting habitat for white-headed woodpeckers (Wightman et al. 2010, Hollenbeck et al. 2011). We quantified landscape heterogeneity using the edge density metric. Edge density, however, contributed minimally to the HSI_{Max} model. Instead, HSI_{Max} mainly reflected a negative relationship with local-scale canopy cover combined with a positive relationship with moderate levels of landscape-scale canopy cover. This combination is consistent with white-headed woodpecker nest placement in relatively open-canopied locations adjacent to more closed-canopied forests where nesting individuals presumably forage (Wightman et al. 2010, Hollenbeck et al. 2011). The HSI_{Mahal} model quantified the average conditions at nest locations (i.e., habitat use) rather than the direction of habitat selection. Average canopy

cover at nest locations did not differ across scales (Table 3), so HSI_{Mahal} could not have portrayed the cross-scale trade-off in relationships with canopy cover.

Habitat selection models, such as HSI_{Max} , may be most effective for predicting species distributions that are mainly determined by habitat selection rather than other population attributes (e.g., dispersal, fitness). High abundance or low availability of desirable habitats may result in substantial use of less desirable habitats, lessening the influence of habitat selection on geographic distribution. Our results suggest use of marginal nesting habitat by white-headed woodpeckers is not substantial enough to negate the predictive value of habitat selection models.

Model Evaluation

Model evaluation criteria provided various insights for interpreting HSI models and extracting useful predictions. Sensitivity (proportion of nests correctly classified high-suitability) and specificity (proportion of the landscape classified low-suitability) provide information on the utility of HSI classification thresholds (Table 5). Lower thresholds designate more nest locations but also more of the landscape as habitat. Thus, lower thresholds are useful if land managers desire liberal estimates of habitat. In contrast, higher

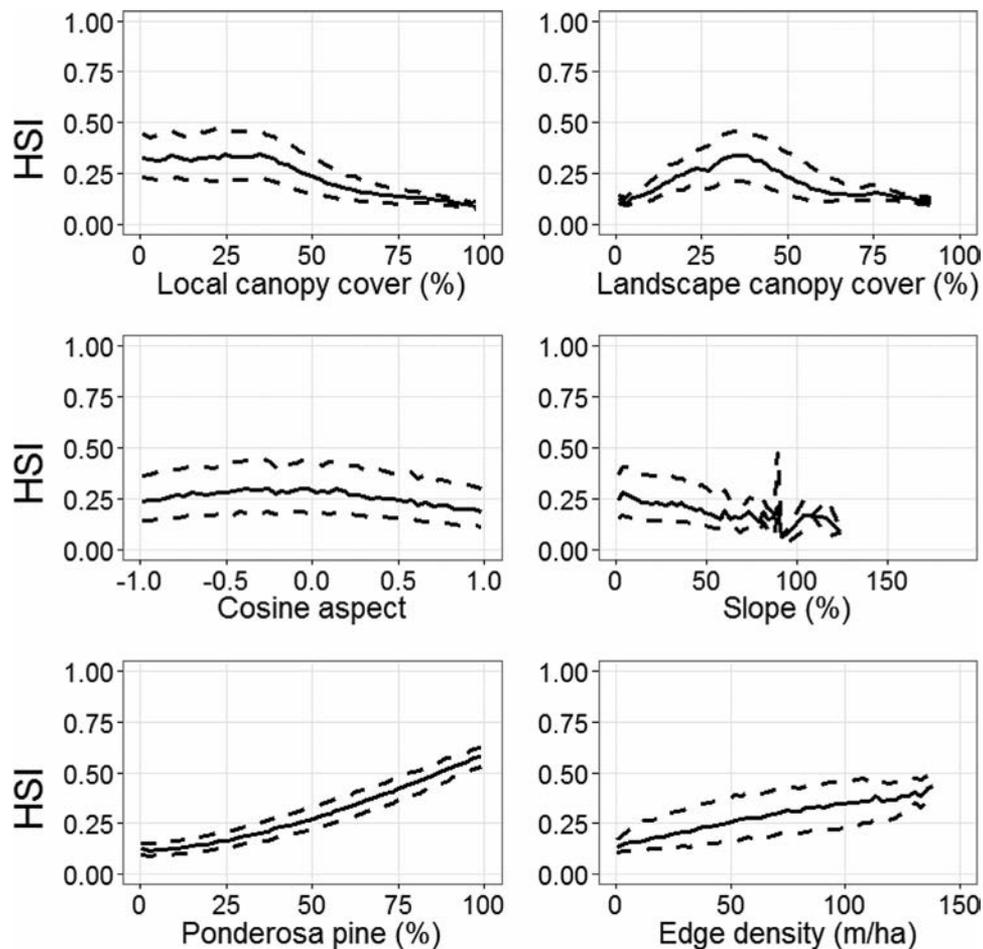


Figure 3. Maxent mean (solid line) and standard deviation (dashed lines) habitat suitability index (HSI) values for nesting white-headed woodpeckers by environmental variables measured in eastern Oregon, 2002 and 2012. We derived means by averaging across 10 replicate models that we used for mapping and evaluating HSIs. The percent contribution of each variable to the model (relative improvement in model fit attributed to the variable) is as follows: local-scale canopy cover = 29.9%, landscape-scale canopy cover = 15.7%, cosine aspect = 10.7%, slope = 0.4%, ponderosa pine = 40.8%, and edge density = 2.5%.

thresholds exclude more of the landscape but also more nest locations from the habitat designation. Thus, higher thresholds correspond to more conservative estimates of habitat. Some HSI_{Max} thresholds that were informative for discriminating nest from available pixels did not perform as well when evaluated with point count data (Table 5). Given that the focus of HSI_{Max} is to characterize habitat selection for nesting, however, we recommend selecting thresholds based upon criteria derived from nest data, that is, the sensitivity and specificity values that correspond with particular management goals. Our confidence in using HSI_{Max} to classify high-suitability versus low-suitability habitat is bolstered by the fact that multiple thresholds performed well when evaluated with independent point count data.

In addition to nest location data, which provided the clearest evidence of breeding habitat use, we also relied on point count data for model evaluation. We assumed that survey points at 300-m spacing were independent based on home range sizes (67–704 ha; Garrett et al. 1996). At this scale, we expected birds to more frequently occupy survey points in areas similar to highly selected or frequently used

locations as indicated by the 2 HSI models we present. This expectation was supported by our data for HSI_{Max} .

Our results suggest consistency in habitat relationships between regions (i.e., East Cascades vs. Blue Mountains) and therefore some transferability of HSI models among areas. Although developed with nest location data from the East Cascade Mountains, HSI_{Max} successfully described habitat use at survey points located in both areas. Generality likely also benefited from using data collected during 2 time periods for model development. Our sample sizes, particularly in the Blue Mountains, however, were limited for detecting regional differences in HSI predictive performance. Additional nest locations from the Blue Mountains would be valuable for further evaluation and refinement of habitat suitability models presented here.

Reliance on remotely sensed data facilitated habitat suitability mapping with greater efficiency and coverage by reducing field effort. Remotely sensed data are limited, however, in their ability to capture fine-scale habitat features potentially important to white-headed woodpecker nesting. For example, we did not incorporate large-tree density despite its importance (Garrett et al. 1996, Hollenbeck et al.

Table 5. Habitat suitability index (HSI) thresholds for classifying low- and high-suitability habitat for nesting white-headed woodpeckers in eastern Oregon, 1997–2004 and 2010–2011. We report the proportion of nest pixels correctly classified highly suitable (sensitivity) and the proportion of the sampled landscape classified low-suitability (specificity; mean [SD] values for 500 and 50 evaluation datasets withheld from model development for Mahalanobis and Maxent models, respectively). We estimated occupancy probabilities with models fitted to point count data (median estimates with 90% Bayesian credible intervals in parentheses).

Model	Threshold	Proportion nests high-suitability	Proportion landscape low-suitability	Occupancy probabilities	
				Low-suitability points with HSIs < threshold	High-suitability points with HSIs > threshold
Mahalanobis D^2	0.21	0.799 (0.112)	0.275 (0.033)	0.38 (0.11, 0.98)	0.55 (0.28, 0.98)
	0.26	0.771 (0.12)	0.313 (0.033)	0.41 (0.12, 0.96)	0.57 (0.27, 0.98)
	0.31 ^a	0.734 (0.125)	0.351 (0.032)	0.40 (0.09, 0.96)	0.61 (0.29, 0.99)
	0.36	0.693 (0.132)	0.388 (0.032)	0.40 (0.15, 0.95)	0.57 (0.28, 0.98)
	0.41	0.643 (0.141)	0.428 (0.032)	0.46 (0.18, 0.98)	0.57 (0.26, 0.99)
	0.46	0.596 (0.136)	0.47 (0.033)	0.42 (0.13, 0.97)	0.62 (0.28, 0.99)
Maxent	0.36	0.828 (0.098)	0.305 (0.067)	0.00 (0.00, 0.09)	0.07 (0.00, 0.71) ^{**}
	0.41	0.728 (0.121)	0.427 (0.061)	0.06 (0.00, 0.51)	0.50 (0.01, 0.95) ^{**}
	0.46 ^a	0.610 (0.108)	0.562 (0.046)	0.35 (0.02, 0.93)	0.56 (0.24, 0.99)
	0.51	0.434 (0.110)	0.700 (0.026)	0.51 (0.19, 0.99)	0.54 (0.26, 0.99)
	0.56	0.295 (0.088)	0.828 (0.010)	0.33 (0.06, 0.87)	0.66 (0.33, 0.99) [*]

^a Thresholds that maximized predictive gain = sensitivity – (1–specificity).

^{*} Bayesian $P < 0.05$, indicating support for a positive β_{HSI} parameter describing the difference in occupancy probability from low- to high-suitability points.

^{**} Bayesian $P < 0.01$. Bayesian $P > 0.15$ for remaining thresholds without any asterisks ($0.05 < P < 0.15$ never occurred).

2011) because of the poor accuracy of GNN-measured tree density ($R^2 < 0.3$, LEMMA 2014), which likely explains its minimal contribution to earlier versions of models presented here (Hollenbeck et al. 2011). Alternative data sources with better resolution (e.g., LiDAR; Lefsky et al. 2002) may provide additional habitat variables useful for improving model predictive performance.

The HSIs we developed have utility for identifying areas to focus habitat conservation and restoration efforts. These HSIs, however, provide limited insight for designing silvicultural prescriptions to improve habitat suitability. Models that describe tree size and characteristics of canopy openings favored for nesting would be better suited for this purpose. Quantification of nesting habitat with sufficient detail to influence management prescriptions will require

both remotely sensed and field-collected environmental data. Such models would be less useful for generating habitat suitability maps but could be combined with HSIs we developed here to provide comprehensive guidance for habitat restoration.

Our study provides models for evaluating how forest restoration or environmental changes (e.g., climate warming) could influence availability of suitable habitat for nesting white-headed woodpeckers. We presented HSI relationships with individual variables across the current landscape, but models that explore interactions of climate, vegetation, and fire are needed to predict future changes to the larger environment (Keane et al. 2011). Assuming no adaptation by the population, researchers could then predict changes to habitat suitability using projected environmental values.

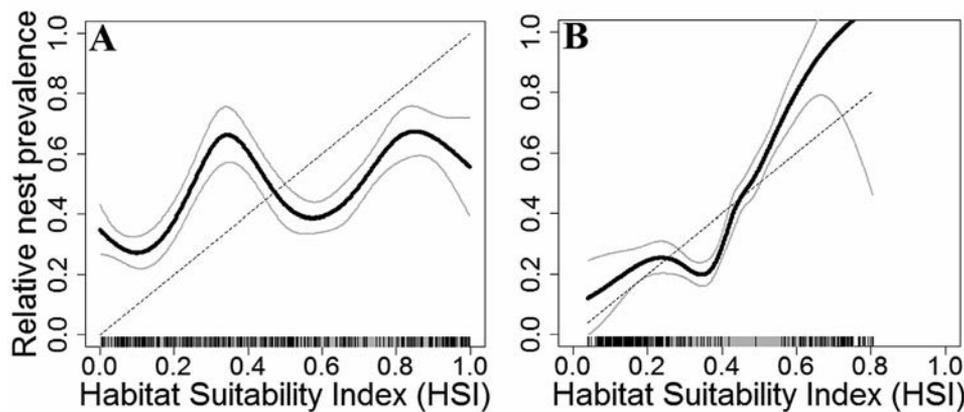


Figure 4. Calibration plots showing habitat suitability index (HSI) relationships with relative nest prevalence (nest prevalence re-scaled to a 0–1 range). We generated HSIs with A) Mahalanobis and B) Maxent models for nesting white-headed woodpeckers in eastern Oregon, 1997–2004 and 2010–2011. We generated plots using 960 nest pixels (10 re-sampled datasets of 96 nests each) and 10,000 available pixels using steps also used to generate data for developing the Maxent model. Calibration curves (black lines) ± 2 standard deviations (gray lines) are from isotonic least squares regression. A curve that lies along the diagonal (dotted line) would indicate an ideally calibrated model. Distributions of nest and available pixels are depicted by gray and black hatches, respectively, along x -axes.

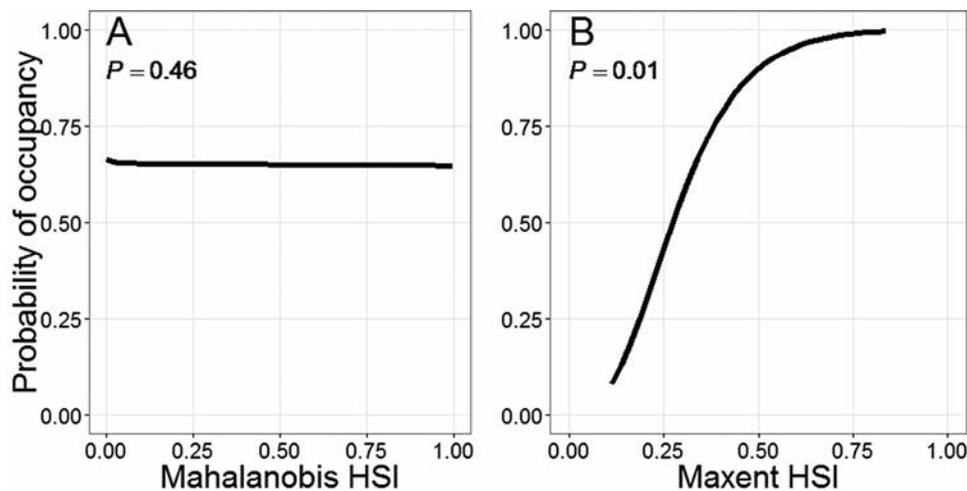


Figure 5. Relationships between probability of occupancy and either A) Mahalanobis D^2 habitat suitability index (HSI) or B) Maxent HSI. We estimated probability of occupancy with models based on point count data for nesting white-headed woodpeckers collected 2010–2012 in eastern Oregon. We report Bayesian P -values representing the statistical support for a positive relationship. A low P -value indicates most of the posterior mass for the slope parameter, β_{HSI} , corresponds with a positive relationship.

Relating HSIs with specific population attributes, such as occupancy rates, abundance, or population dynamics, would facilitate predictions of likely population responses expected with changes in habitat suitability.

MANAGEMENT IMPLICATIONS

To improve reliability and to effectively inform management, discrete HSI classifications may be more desirable than continuous HSIs. We identified several thresholds from which managers can choose to meet specific objectives. If a management goal is conservation of only the highest suitability habitat, we suggest using higher thresholds. Alternatively, if conservation is focused on providing the most acres of potentially suitable habitat, lower thresholds would be more appropriate. Restoration efforts could target lands with potential for habitat improvement identified by HSI scores below specified thresholds. Areas characterized as low-suitability would need to be field assessed to determine if management prescriptions would be beneficial. Additionally, because HSIs were in part derived from variables describing 1-km neighborhoods, management plans must take into account the area surrounding a location to maintain or improve habitat suitability at that location. Models presented here are based on areas in the Inland Pacific Northwest where white-headed woodpeckers require ponderosa pine forests (i.e., eastern Oregon and Washington, and western Idaho), and should be applied only in areas with at least some ponderosa pine (>10% within 314 ha). Alternative models would be needed in areas where ponderosa pine is not dominant (i.e., in California; Milne and Hejl 1989, Alexander and Burns 2006).

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