



Conservation and relative habitat suitability for an arboreal mammal associated with old forest



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ABSTRACT

Contraction of native old forest can limit occurrence of old forest associated species, especially species with limited vagility. Patterns of size and distribution of remaining patches of old forest along with forest disturbance and what replaces old forest can influence whether species adapt or perish after forest loss. The arboreal red tree vole (*Arborimus longicaudus*) is a small arvicoline rodent that is associated with old coniferous forest and typically emigrates short distances. Since 1911, old forest (≥ 80 years old) in the northern half of the Oregon Coast Range has been reduced by $>80\%$, primarily due to large stand replacing wildfires, timber harvest, and subsequent conversion to young forest (<80 years old). In 2011, the tree vole population in the northern half of the Oregon Coast Range was listed as a candidate species as a distinct population segment under the United States Endangered Species Act, primarily due to habitat loss. We examined the contribution of current and historical (early 20th century) old forest cover, and recent disturbances (1984–2012) on relative habitat suitability for tree voles using light detecting and ranging (LiDAR) data, Landsat imagery, and machine learning. We used a step-wise variable removal procedure to build a parsimonious model and to rank contribution of variables in our final model. We further described the configuration of large patches of old forest using metrics of amount and distance from patch for historical, current, two forest loss scenarios, and two forest restoration scenarios within our study area. Red tree vole relative habitat suitability was positively correlated with current old forest cover at the local-scale and negatively correlated with distance from large patches of current old forest. Landscape context, specifically proximity to old forest and absence of recent disturbance contributed most to relative habitat suitability of young forest matrix. If old forest contracted to only reserves on federal lands, amount would decrease from 10.9% to 9.5% and be spatially clumped with an increase in average distance to nearest patch from 3.1 km to 11.1 km. Alternatively, a random addition of patches equivalent to a 1.4% increase in amount, would reduce distance to nearest patch to 1.8 km. Given the history of large historical wildfires in the Oregon Coast Range, restoration of even a small amount of old forest throughout the study area would likely enhance connectivity and resiliency of red tree vole populations in the event of large-scale loss of old forest.

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1. Introduction

Globally, native old forest ecosystems have contracted in area and have been highly altered by human actions, and this is the case of old forest in the Pacific Northwest (Hansen et al., 1991; Noble and Dirzo, 1997). For old forest associated species, the amount and configuration of remaining old forest, what replaces old forest, and the species' life history traits are the main drivers of whether species adapt or perish in altered forest ecosystems (Fahrig, 2001; Franklin, 1993; Kupfer et al., 2006; Ruffell et al., 2017; Selonen and

Hanski, 2003). Matrix, or background cover types in which old forest resides, can influence species' dispersal, movement, and population-level processes by either enhancing or limiting species persistence, often depending on its resemblance or contrast to pre-existing old forest (Franklin, 1993; Greene and McCleery, 2017; Prevedello and Vieira, 2010; Ritchie et al., 2009; Ruffell et al., 2017).

Arboreal mammals may be particularly sensitive to contraction of native old forest because they often depend on structural or ecological characteristics of old trees that take decades or centuries to develop (Banks et al., 2013; Forsman et al., 2016). Where young forest replaces old forest, young forest can complement remaining old forest (Andr en, 1994; Franklin, 1993; Kupfer et al., 2006). If

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young forest can facilitate emigration, survival, and reproduction for old forest associated species, albeit at potentially lower rates than old forest, young forest may function as low-contrast matrix and increase the footprint of dispersed patches of old forest.

The arboreal red tree vole (*Arborimus longicaudus*, hereafter tree vole) is a small arvicoline rodent endemic to western Oregon and northwest California that depends entirely on coniferous forests for life history requirements. Tree voles build nests on complex branch and bole structures consisting of broken tops, cavities, palmate branch whorls, large limbs, forked trunks, and dense limb whorls that are near fresh conifer needles that they feed on (Benson and Borell, 1931; Howell, 1926; Maser, 1966; Swingle, 2005). Tree vole habitat models have shown a strong association with old forest (≥ 80 years old) characteristics where complex branch and bole structures are most prevalent (Dunk and Hawley, 2009; Forsman et al., 2016; Johnston and Moskal, 2017; Spies and Franklin, 1991). Some have suggested that young forest (<80 years old) is non-habitat or marginal habitat for tree voles (Aubry et al., 1991; Carey, 1991; Huff et al., 1992). However, many have found populations of tree voles in young forest (20–80 years old; Clifton, 1960; Maser, 1966; Swingle and Forsman, 2009; Thompson and Diller, 2002). Fragmentation models that delineate hard boundaries between habitat and non-habitat do not account for the potential contribution of low-contrast matrix as habitat (Fischer and Lindenmayer, 2006). Proximity to old forest may constrain occurrence of tree voles in young forests because, on average, tree voles do not move or disperse far (<60 m; Swingle, 2005; Swingle and Forsman, 2009).

In the Oregon Coast Range, the amount of old forest consisting of mature (80–200 years old) and old-growth (>200 years old) forest (Spies and Franklin, 1991) was reduced from 36% to 13% in the period from 1936 to 1993, and is currently estimated to be outside the lower limits of natural variability (Kennedy and Spies, 2004; Wimberly et al., 2000). Old forest currently occurs as smaller and more isolated patches within a matrix primarily composed of young forest, compared to larger blocks that historically occurred (Forsman et al., 2016). Forest age largely differs across ownership boundaries (Stanfield et al., 2002) with most old forest occurring on federal lands managed by the USDI Bureau of Land Management and the USDA Forest Service, most of which is protected as old forest reserves as habitat for the threatened northern spotted owl (*Strix occidentalis*) and other old forest associated species (Davis et al., 2015; USDA and USDI, 1994). Primarily because of habitat loss (i.e., old forest), the tree vole population in the Oregon Coast Range north of the Siuslaw River was recognized as a distinct population segment and listed as a candidate species for protection under the United States Endangered Species Act in 2011 (USDI, 2011).

We examine the contribution of current old forest, young forest, and historical forest cover patterns on relative habitat suitability for tree voles in the entirety of the area containing the distinct population segment. We began with the premise that old forest was likely to be primary habitat at the local- and landscape-scale (120 m and 1 km radius, respectively) for tree voles (Dunk and Hawley, 2009; Forsman et al., 2016). We also predicted that: (1) if tree vole occurrence in young forest was due to emigrants originating from patches of old forest (>20 ha) estimated to support a small population of 1.0–1.9 tree voles per ha (Maser, 1966; Marks-Fife, 2016), then relative habitat suitability would diminish with distance from these patches, (2) recent removal or alteration of forest cover would decrease relative habitat suitability because site-level occurrence of tree voles is dependent on intact forest cover; and (3) if large historical disturbances from the early 20th century where old forest was removed limited recolonization by tree voles, then current tree vole occurrence would decrease with distance from historical 1911 and 1936 old forest cover

(Harrington, 2003; Oregon State Board of Forestry, 1914). Finally, we described landscape configuration using amount, mean size, and minimum distance from patches of old forest (Prugh et al., 2008) to compare configuration of old forest cover in historical (1911, 1936, and 2015), two forest loss scenarios (if old forest contracted to old forest management areas on state and federal vs. only federal lands), and two restoration scenarios.

2. Data and methods

2.1. Study area

The study area contained the distinct population segment within the historical range of the tree vole in the northern half of the Oregon Coast Range (Fig. 1). The area contained approximately 16,000 km² of forested land (Forsman et al., 2016). Most coniferous forest in the study area was dominated by Douglas-fir (*Pseudotsuga menziesii*) with a narrow zone along the coast dominated by western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*). Stands of red alder (*Alnus rubra*) and bigleaf maple (*Acer macrophyllum*) occurred throughout the study area. The climate was characterized by cool wet winters and warm dry summers with areas of summer fog (Franklin and Dyrness, 1973). Natural disturbance consisted of infrequent but large, high-severity wildfires (Wimberly et al., 2000). In the early 20th century, the four large wildfires of the 1931–1951 Tillamook Burn (Highsmith, 1952) and clear-cut harvesting denuded old forest in the northern portion of the study area, including areas now managed by the state of Oregon north of the Nestucca River (ODF, 2010). Forests were primarily managed by private owners (60%) and federal agencies (23%; Forest Service and Bureau of Land Management) with state and local government (15%) and Native American tribes (2%) managing the remainder. Most state forest lands occurred north of the Nestucca River and most federal lands to the south (Fig. 1).

Most background cover types (matrix) consisted of intensively managed young forests of Douglas-fir of varying age originating after clear-cut timber harvest (Lorenson et al., 1994). Private forests were typically managed with short harvest rotations (40–60 years) and state forests were managed with longer rotations up to 80 years (Adams et al., 2002; Oregon Department of Forestry, 2006). Some state forest lands were managed as anchor habitat for site-specific protection for species of concern to maintain some old forest structure within a shifting mosaic design over time (Oregon Department of Forestry, 2010). Federal land management within the study area followed the Northwest Forest Plan from 1994 to 2015 (USDA and USDI, 1994). The Northwest Forest Plan created reserves to enhance and maintain old forest conditions as habitat for the northern spotted owl, marbled murrelet (*Brachyramphus marmoratus*), and other old forest associated species. Areas of old forest outside of federal reserves have been subject to timber harvesting if Survey and Manage species, including the tree vole, were not detected (Huff et al., 2012; Huff, 2016; USDA and USDI, 1994). Much of the most recent harvesting on federal lands has focused on young forest and typically consisted of commercial thinning.

2.2. Tree vole data

Our data consisted of tree vole nests located during 2000–2015. We used data collected during research surveys conducted on state, federal, and private lands (Forsman et al., 2016) by the Forest Service's Pacific Northwest Research Station and data collected on federal lands as part of "pre-disturbance," "purposive," and "strategic" surveys conducted by the Bureau of Land Management and Forest Service as part of the Northwest Forest Plan Survey and

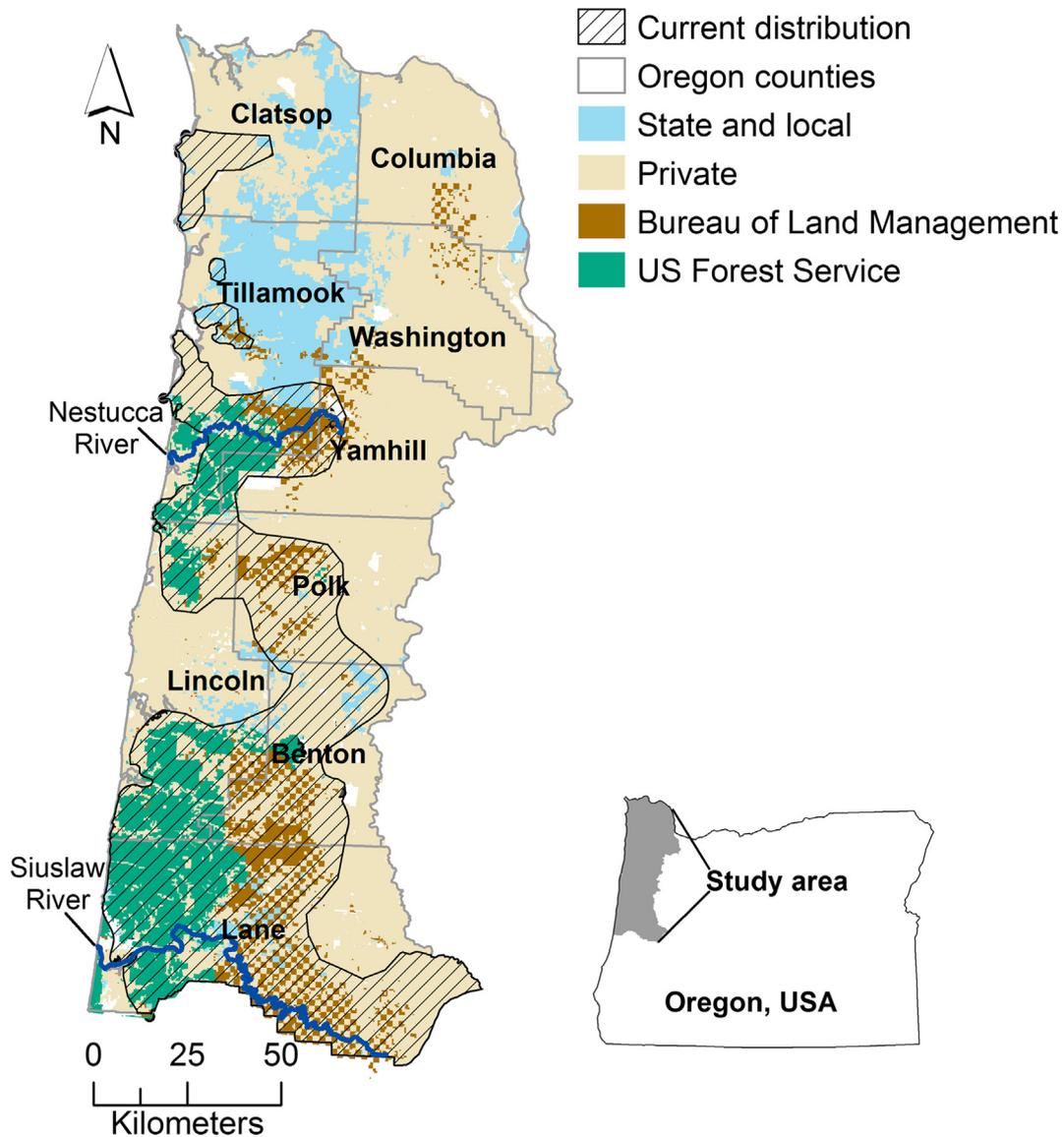


Fig. 1. Study area showing the northern portion of the historical range (outer boundaries), current distribution of red tree voles (Forsman et al., 2016), and land ownership in the northern half of the Oregon Coast Range, USA.

Manage program. In sum, we used 1,752 tree vole nest locations from those sources and survey effort was relatively well distributed across our study area (Forsman et al., 2016). The primary technique for collecting tree vole nest location data was to visually locate potential nests from the ground and then climb trees to confirm tree vole nest material consisting of resin ducts, debarked twigs, conifer cuttings, and fecal pellets (Benson and Borell, 1931; Clifton, 1960; Maser, 1966). A less-used technique was to survey individual trees for tree vole nests while tree climbing (Dunk and Hawley, 2009; Forsman et al., 2016; Huff et al., 2012).

As most of the tree vole location data were collected with global positioning units, the spatial accuracy was assumed to be less than 30 m and was smaller than the smallest pixel size used in our geographic information systems analysis (30 × 30 m). We used aerial photos to visually evaluate tree vole nest locations to ensure each location actually occurred within forest, had not been harvested, or otherwise disturbed between the time of discovery and time of data collection of remotely sensed data. Because many of the tree vole nest locations were clustered due to survey methods, we used spThin package in program R (Aiello-Lammens et al., 2015; R Core Team, 2013), to spatially disperse the location data to ensure mod-

eling data were independent. We selected 1 km as the thinning threshold as it was three times the maximum straight-line distance of a documented tree vole movement (Biswell and Meslow, 1994) and because clustered nest locations from the same survey were often separated by <300 m. After thinning nest location data, we used the resulting 233 tree vole locations for model training and analysis.

2.3. Environmental variables

Remote sensing has been increasingly used for evaluating forest conditions and species distribution modeling, and resulting maps have proved to be useful tools for species conservation management (He et al., 2015). Most recently, the use of airborne light detecting and ranging (LiDAR) data have improved upon the accuracy of these products by providing a high-resolution snapshot of forest condition (Ackers et al., 2015; Gastón et al., 2017; Vogeler and Cohen, 2016). The ability to directly measure height and structural configuration of forest vegetation at high spatial resolutions makes LiDAR a valuable data source for studying habitat relationships of forest dwelling canopy species and for using that informa-

tion to produce spatially explicit habitat maps (Vogeler and Cohen, 2016). LiDAR data are now available for broad landscapes, and thus may be well-suited for development of tree vole habitat models because forest cover and other metrics can be examined at a broader landscape scale while retaining local-scale resolution (Forsman et al., 2016; Johnston and Moskal, 2017).

We used airborne LiDAR data acquired during 2006–2016 that we obtained from the Oregon Department of Forestry, Bureau of Land Management, and Forest Service; and Landsat data acquired from Forsman et al. (2016), Moeur et al. (2011) and Kennedy et al. (2010). Specifically, we used a Landsat satellite imagery data (<http://landsat.usgs.gov/>) change detection algorithm which detects changes in annual satellite imagery (Landtrendr; Kennedy et al., 2010) to model disturbance history (1984–2015) and gradient nearest neighbor (GNN) satellite data developed by the Landscape Ecology, Modeling, Mapping, and Analysis group (<http://lemma.forestry.oregonstate.edu>) to model forest structure and composition (Ohmann and Gregory, 2002). The LiDAR data, consisting of first laser returns representing highest height and last returns representing the bare earth, were accessed in program ArcGIS (Environmental Systems Research Institute, Redlands, CA). Depending on the LiDAR layers, pixel size was either 0.5 or 1.0 m and tree height accuracy was estimated to be <1.2 m in a small portion of our study area (Edson and Wing, 2011). We mosaicked all LiDAR layers, and used the minimum height of vegetation at overlapping pixels to account for potential forest disturbance between LiDAR collection dates. Finally, we resampled, and aligned all data layers to 30 × 30 m pixels, and masked out any non-forest landscape pixels within our study area (e.g. rivers, agricultural lands).

We identified height thresholds for forest cover at two age classes: >20 years old (AllForest; >12.6 m) and ≥80 years old (OldForest; >37 m) using a regression of tree height with tree age using data from the Forest Inventory Analysis Program data (USDA, 2015). We used a combined mean height of the three most common conifers used by tree voles in our study area (Douglas-fir, western hemlock, and Sitka spruce). We selected >20 years old because this is the minimum age that tree voles have been documented to recolonize regenerating forest. At 80 years of age trees start to form substantial quantities of structures on which tree voles and other arboreal rodents can build nests (Forsman et al., 2016; Spies and Franklin, 1991). To simplify models by limiting the number of variable combinations, we combined mature (80–200) and old-growth forest (>200 years old) into one old forest age-class (Merow et al., 2014). We used a moving window with two extents of 120 m or 1 km, and calculated the percentage of OldForest or AllForest cover (Table 1).

To delineate patches of old forest cover for use with the PatchDist2015 variable, we selected blocks of pixels >20 ha in size where the pixel value was >30% old forest cover within a 120 m moving

window. We selected >30% forest cover at the pixel-level as our threshold for inclusion because tree voles will use forest edge. We identified >30% forest cover as the value where the edge of the patch was smoothed and inclusive by comparing our OldForest layer to known patches of old forest (Forsman et al., 2016; aerial photos), resulting in a mean ± standard deviation of old forest pixels within patches of 50% ± 15%. Finally, we calculated Euclidean distance to these patches. We repeated this final step to estimate distance from historical >20 ha patches in 1911 and 1936 (PatchDist1911 and PatchDist1936; Forsman et al., 2016), and >20 ha patches within current old forest management areas. The historical 1914 forest map consisted of field surveys and county records (Oregon State Board of Forestry, 1914) and the 1936 map was based on interpretation of aerial photos, county records, and field surveys (Andrews and Cowlin, 1940; Harrington, 2003). We mapped the percentage of forest disturbance within a 120 m moving window (Disturb120 m) during the period 1984–2012 using the Landtrendr algorithm and percentage of hardwoods (Hardwood120 m) also within 120 m moving windows. We tested collinearity between variables and removed the variable that contributed least to model performance if two variables were highly correlated based on pairwise correlation coefficient (r) > 0.7 and variance inflation factor > 5, (Dormann et al., 2007; Fielding and Bell, 1997).

2.4. Habitat modeling

We used program MaxEnt (Phillips et al., 2006), which uses presence-only data and machine learning, to model relative habitat suitability of tree voles within our study area. MaxEnt produces spatially explicit predictions, based on model output and conditions at each map pixel. MaxEnt functions by minimizing the entropy or differences between the average conditions obtained at 10,000 randomly-sampled pixels within the study area (background data) and conditions at pixels where tree vole nests were observed. We assumed that our random sample was representative of conditions present in our study area, and therefore, we interpreted MaxEnt's logistic model output as relative habitat suitability (Merow et al., 2013; Royle et al., 2012). Following Phillips and Dudík (2008), we used modeling features to fit environmental variables to tree vole presence data. To minimize complexity of our models, we limited our set of features to linear, and pairwise products of covariates (Merow et al., 2013; Phillips et al., 2006).

To produce a final model, we used a three-stage process: (1) we used a step-wise variable removal procedure to identify the combination of variables with highest model performance, (2) we compared model performance between consecutive models with one fewer variable to identify how many variables to include, and (3) we used the regularization multiplier to optimize the model such

Table 1

Predictor variables used for red tree vole habitat modeling are ranked in order of removal at each iteration of model fitting. Additionally, we present the percent contribution of each variable in the global model. The study occurred in the northern half of the Oregon Coast Range, USA.

Variable description	Source	Prediction direction	Variable code	Iteration	Percent contribution
Distance from >20 ha patch of old forest cover in 1911	Historical ^a	–	PatchDist1911	1	0.8
Percentage of forest cover >12.6 m high within 1 km	LiDAR	+	AllForest1 km	2	2.9
Percentage of forest cover >12.6 m high within 120 m	LiDAR	+	AllForest120 m	3	7.3
Distance from >20 ha patch of old forest cover in 1936	Historical ^a	–	PatchDist1936	4	1.7
Percentage of old forest cover ^c within 1 km	LiDAR	+	OldForest1 km	5	3.6
Percentage of hardwood cover within 120 m	Landsat	–	Hardwood120m ^b	6	3.4
Percentage of forest disturbance (1984–2015) within 120 m	Landsat	–	Disturb120m ^b	7	17.9
Distance from >20 ha patch of old forest cover ^c in 2015	LiDAR	–	PatchDist2015 ^b	8	13.9
Percentage of old forest cover ^c within 120 m	LiDAR	+	OldForest120m ^b	9	48.3

^a Maps created from historical survey data.

^b Variable included in final model.

^c Old forest cover defined as forest cover >37 m high.

that it was not over- or under-fit. In our first stage, we used an iterative variable removal process to identify our best performing variables by removing the least informative variable at each modeling step (Table 1). We fitted each model at this stage with the regularization multiplier setting constant at 1.0. To estimate test statistics for each iteration, we performed a series of bootstrapped models with 10 replicates. Each replicate used a random sample consisting of 75% of tree vole presence data to train the model and 25% to test model prediction. We used jack-knife graphs of mean test gain and area under the receiver operating curve (AUC) from bootstrap replicates, and dropped the variable that produced the highest gain in model performance when omitted (Yost et al., 2008). AUC is scaled from 0–1, and AUC values of 0.5 indicate no discrimination (no better than random chance). Specific to our modeling, results from AUC represented the proportion of times that a location with tree vole nest presence would have a higher relative habitat suitability value than a randomly selected background location.

In the second stage, we compared model performance by noting a statistically significant drop in 95% confidence intervals for test AUC and training gain statistics between consecutive model iterations (Swets, 1988; Yost et al., 2008). We used the variables contained in the model prior to the statistical drop in one or more of test AUC and training gain in our final model. We evaluated final model performance using the continuous Boyce index (CBI; Hirzel et al., 2006) that is based on the Spearman's rank correlation coefficient and adapted specifically for presence-only habitat models.

In the third stage, we adjusted the regularization multiplier step-wise 0.5 to 5.0 at intervals of 0.5. For each step, we evaluated differences in the 95% confidence intervals of training and test gain, AUC, and CBI. The regularization multiplier performs a function similar to Akaike information criterion by penalizing complex models. Specific to MaxEnt, higher values of the regularization multiplier penalize complex models that include combinations of features and environmental variables that contribute little to model fit but that may over-fit the data (Halvorsen et al., 2015). We selected the final model where the regularization multiplier setting produced a model with the highest test AUC and CBI, and similar test and training gain. We report the percentage of contribution of each variable in the global model and final model.

2.5. Habitat mapping

Once we had a final model, we used the predicted-to-expected (P/E) ratio curve, produced from CBI, to evaluate final model performance and to reclassify continuous model output at each map pixel into four relative habitat suitability classes (Hirzel et al., 2006). At a value of P/E = 1 density of tree vole nest locations is predicted to be no higher than random chance. A good model consistently discriminates presences as relative habitat suitability increases and is indicated by a monotonically increasing P/E curve. We used the 95% confidence intervals of the P/E curve to identify four discrete classes: unsuitable, marginal, suitable, and highly suitable. We assumed P/E values no better than random (upper 95% CI of P/E < 1) were unsuitable, P/E values overlapping 1 were marginal (95% CI overlaps P/E = 1), and then divided the remaining values (lower 95% CI of P/E > 1) in half – the lower remainder being suitable and the highest 50% as highly suitable (upper 50% of P/E > 1).

2.6. Landscape analysis

Since tree voles are thought to be associated with old forest, we explored simple landscape configuration metrics consisting of amount of old forest cover, patch size of old forest, and mean distance from >20 ha patch of old forest for historical (1911 and

1936), current (2015), current old forest management areas, and two restoration scenarios within our study area. We had two scenarios for current old forest management areas based on land ownership: (1) federal reserve lands that were managed to maintain late-successional forest conditions and that were protected from timber harvest (1994 to 2015; USDA and USDI, 1994) plus state lands consisting of anchor habitat that were site-specific protection for species of concern (Oregon Department of Forestry, 2010), and (2) only federal reserve lands. Finally, we simulated restoration of old forest patches within the study area by randomly generating old forest patches, assuming patch size was equal to the mean patch size in the current landscape (1.4 km²), in an amount equal to the percentage of old forest lost if old forest contracted to old forest management areas. All means are reported as $\bar{x} \pm 1$ standard deviation.

3. Results

Of the 233 nest locations used in the final model, most were located within (41%) or near (0.1–2.0 km) to >20 ha patches of old forest (53%). Few nest locations were entirely in young forest with no old forest cover within 120 m (9%) and these locations were on average 0.7 ± 0.6 km from a >20 ha patch of old forest. Tree vole nest locations were consistently in areas of extensive forest cover at the landscape (1 km) and local-scale (120 m) as measured by OldForest and AllForest variables compared to random background points (Table 2).

The final model was fitted with four variables (Table 1) using a regularization multiplier setting = 4.0, which produced an AUC = 0.84 ± 0.02 and a CBI = 0.95 ± 0.03 . The mean P/E value (3.0) of suitable pixels was approximately 30 times higher than the mean P/E value of unsuitable pixels (0.1; Fig. 2). No variables were removed because of collinearity and variance inflation factors were all < 1.5. Our maximum correlation for variables in our final model was -0.35 (OldForest120 m, Disturb120 m). Individual variable response curves (Fig. 3) matched our *a priori* predictions (Table 1). At the local-scale, our model indicated that relative habitat suitability increased with percentage of old forest cover and decreased with distance to current patches of old forest (Fig. 3). Old forest cover at the local-scale (49.4%), disturbance (30.3%), and distance to old forest patch (16.6%) contributed most to final model fit as measured by percent contribution (%). Historical old forest cover and the percentage of forest cover >12.6 m were relatively less important than other variables (Table 1). Forest on federal lands comprised 63% of the combined total of predicted suitable and highly suitable habitat in the study area, and forest on private lands comprised 73% of the combined total of predicted unsuitable and marginal habitat (Fig. 4). Private, state, and local lands, nonetheless, contained some highly suitable predicted habitat including >20 ha patches of old forest cover (Fig. 4; Fig. 5a, c). Our model predicted areas of suitable habitat north of the Nestucca

Table 2

Summary statistics for 10,000 randomly generated background points and presence-only nest locations for red tree voles in the northern half of the Oregon Coast Range, USA. Results are reported as mean ± 1 standard deviation.

Variable (units)	Random ($n = 10,000$)	Presence ($n = 233$)
PatchDist1911 (km)	0.7 ± 1.9	0.7 ± 1.3
AllForest1 km (%)	40.0 ± 30.9	67.0 ± 18.0
AllForest120 m (%)	41.0 ± 38.0	79.1 ± 18.8
PatchDist1936 (km)	1.1 ± 2.9	0.6 ± 1.0
OldForest1 km (%)	9.3 ± 11.3	18.8 ± 12.5
Hardwood120 m (%)	14.4 ± 20.5	14.4 ± 17.5
Disturb120 m (%)	29.7 ± 37.9	11.8 ± 21.3
PatchDist2015 (%)	2.6 ± 4.9	0.6 ± 2.2
OldForest120 m (%)	6.8 ± 15.1	31.2 ± 22.0

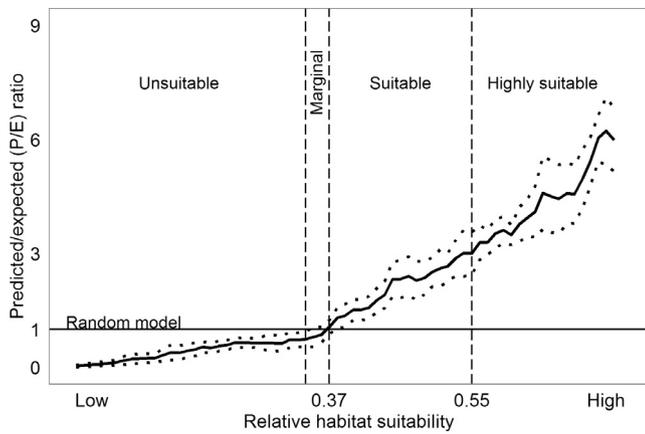


Fig. 2. Predicted to expected ratio results used to classify relative habitat suitability (Hirzel et al., 2006) for red tree voles from mean continuous data (black line) and 95% confidence intervals (dots) in the northern half of the Oregon Coast Range, USA. Line at $P/E = 1$ represents the performance of a completely random model.

River that are outside of the current distribution of the tree vole but within the historical range (Fig. 5c; Forsman et al., 2016).

Old forest cover in our study area contracted by >80% in extent from 1911 to 2015 from 56.1% to 10.9% of the study area (Table 3), and would contract further if areas managed for old forest conditions were eliminated (Fig. 6). An additional 0.8% loss of old forest would occur if old forest on non-old forest management areas and private lands were eliminated, and the average distance from patches of old forest cover would increase from 3.1 to 5.1 km. If no state lands were managed in old forest conditions, a further reduction of 0.6% would occur and average distance from patches would increase to 11.1 km, an approximately threefold increase compared to the 2015 landscape. Alternatively, an increase of 1.4% in number of old forest patches to the current study area (2015) in our restoration scenario would result in a 1.3 km average decrease and reduced variability in distance from patch (Table 3). Patches in this scenario were randomly placed outside of old forest in the current study area and were disproportional to available land by ownership within the study area for private (79% vs. 60%) and for federal lands (5% vs. 23%) but proportional for state lands (16% vs. 15%), respectively.

4. Discussion

Our results suggest that contraction of old forest has substantially shaped and constrained the current distribution of tree voles in the northern half of the Oregon Coast Range (Forsman et al., 2016). Consistent with previous modeling (Dunk and Hawley, 2009; Forsman et al., 2016; Johnston and Moskal, 2017;

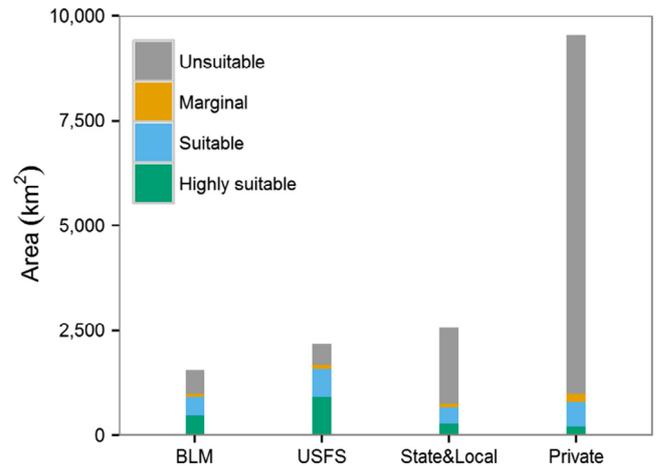


Fig. 4. Amount of land area (km^2) by ownership subdivided by relative habitat suitability classes for red tree vole in the northern half of the Oregon Coast Range, USA. BLM = Bureau of Land Management. USFS = Forest Service.

Rosenberg et al., 2016), old forest cover at the local-scale was the strongest predictor. Old forest appeared to drive patterns of relative habitat suitability in our study area: (1) old forest at the local-scale was the most important predictor in our final model, (2) relative habitat suitability of young forest matrix was limited by proximity to current >20 ha patches of old forest and recent disturbance, and (3) relative habitat suitability was more highly correlated with recent timber harvest disturbances than distance to historical large disturbances shown in 1911 and 1936 maps. Tree vole association with current old forest provided further evidence that relative habitat suitability of young forest was limited by landscape context but could potentially complement extant old forest if located in close proximity. Finally, given the rarity of existing patches of old forest and that even small reductions of 0.8% and 1.4% within the current study area dramatically increased distance to nearest patch, tree voles are likely to remain vulnerable to extirpation in areas of the distinct population segment, especially north of the Nestucca River.

Landscape context, specifically proximity to old forest and absence of recent disturbance (1984–2012) contributed most to predicted suitability of young forest matrix. The contrast between young and old forest is likely to swing dramatically under current forest practices, alternating from potentially suitable habitat consisting of young forest >20 years old to unsuitable following clear-cut and commercial thinning harvests. Although we identified 20 ha of old forest as a relevant patch size for tree voles, even small amounts of adjacent low-contrast young forest may effectively function to increase the patch size of old forest (Andrén,

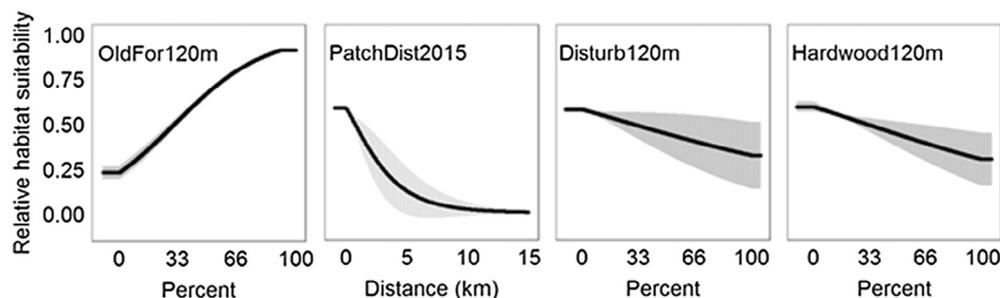


Fig. 3. Mean univariate model response functions (black line) and 95% confidence intervals (gray shading) between predictor variables and relative habitat suitability for red tree voles in the northern half of the Oregon Coast Range, USA. OldFor120m = percentage of old forest cover >37 m within 120 m, PatchDist2015 = distance from >20 ha old forest source patch in 2015, Disturb120m = percentage of forest disturbance (1984–2015) within 120 m, and Hardwood120m = percentage of hardwood cover within 120 m.

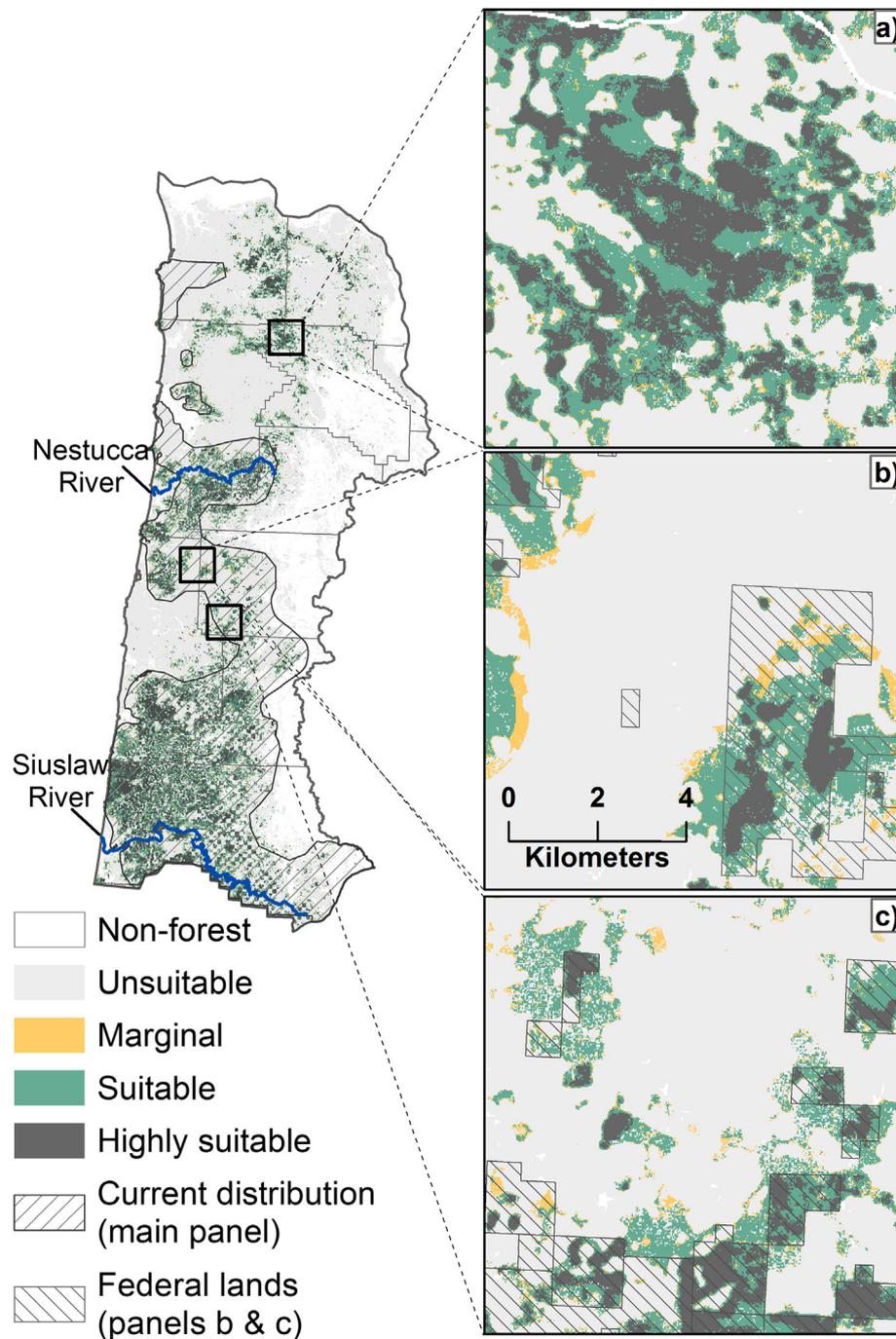


Fig. 5. Red tree vole relative habitat suitability subdivided into four classes using the predicted-to-expected ratio curve from logistic model output displayed across ownership in the northern half of the Oregon Coast Range, USA. We show three examples of our model: (a) predicted suitable habitat outside of the current extent of the red tree vole range where historical large disturbances potentially limited recolonization, (b) old forest reserve centrally located on federal lands within the study area, (c) potential contribution of intervening patches of old forest on nonfederal land that could act as a potential link with old forest management areas on public lands.

1994; Ruffell et al., 2017). Matrix permeability is highly dependent on forest age and structure (Prugh et al., 2008). For tree voles, our modeling results suggest that temporal and spatial barriers to movement occur when the matrix consists of extensive recently disturbed forest, including forest cover <20 years old or commercially thinned young forest (Forsman et al., 2016; Wilson and Forsman, 2013).

Tree vole emigration from old forest to young forest post-disturbance may be a particularly important mechanism for tree vole persistence, emphasizing the importance of proximity to remnant patches of old forest. Yet, few studies have examined the

importance of refugia in recolonization after large scale disturbance. In semi-arid shrublands of Australia, even small unburnt remnants (>5 ha) within post-fire landscapes contributed to immediate (2 years) post-fire recovery of bird populations (Watson et al., 2012). Alternatively, individuals that survived wildfires by taking refuge in unburned areas likely contributed to immediate colonization by an insectivorous marsupial and an omnivore in Australian temperate forests (Banks et al., 2011). Clear-cut timber harvesting eliminates tree voles and their habitat, and similar response to forest removal was observed for an arboreal Australian folivore (Tyndale-Biscoe and Smith, 1969). Large remnant trees in young

Table 3
Landscape configuration metrics of old forest cover (≥ 80 years old) for three landscapes in 1911, 1936, and 2015, two old forest management areas, and two restoration scenarios in the northern half of the Oregon Coast Range, USA. Old forest management areas are managed to maintain old forest conditions on federal and state lands (Fed + State) and only federal lands (Fed). Restoration scenarios (2015 + 0.8% and 2015 + 1.4%) were simulated by randomly increasing the number of patches in an amount equal to the percentage of old forest lost if old forest contracted to federal and state lands managed for old forest conditions (0.8%) or just to federal lands managed for old forest (1.4%). We summarized all pixels classified as forest land-use within the study area.

Landscape metric	1911	1936	2015	Fed + State ^a	Fed	2015 + 0.8%	2015 + 1.4%
Old forest amount	56.1%	39.2%	10.9%	10.1%	9.5%	11.7%	12.3%
Distance to old patch (km) ^b	1.0 \pm 2.1	1.5 \pm 3.3	3.1 \pm 4.7	5.1 \pm 6.1	11.1 \pm 15.6	2.1 \pm 2.8	1.8 \pm 2.2
Number of patches	160	328	1274	968	908	1368	1438
Mean patch size (km ²) ^b	56.1 \pm 326.4	19.1 \pm 156.1	1.4 \pm 4.7	1.7 \pm 5.7	1.7 \pm 5.8	1.4 \pm 4.6	1.4 \pm 4.5

^a State anchor habitat and federal reserve land-use allocations for site-specific protection for species of concern.

^b Reported as mean \pm 1 standard deviation.

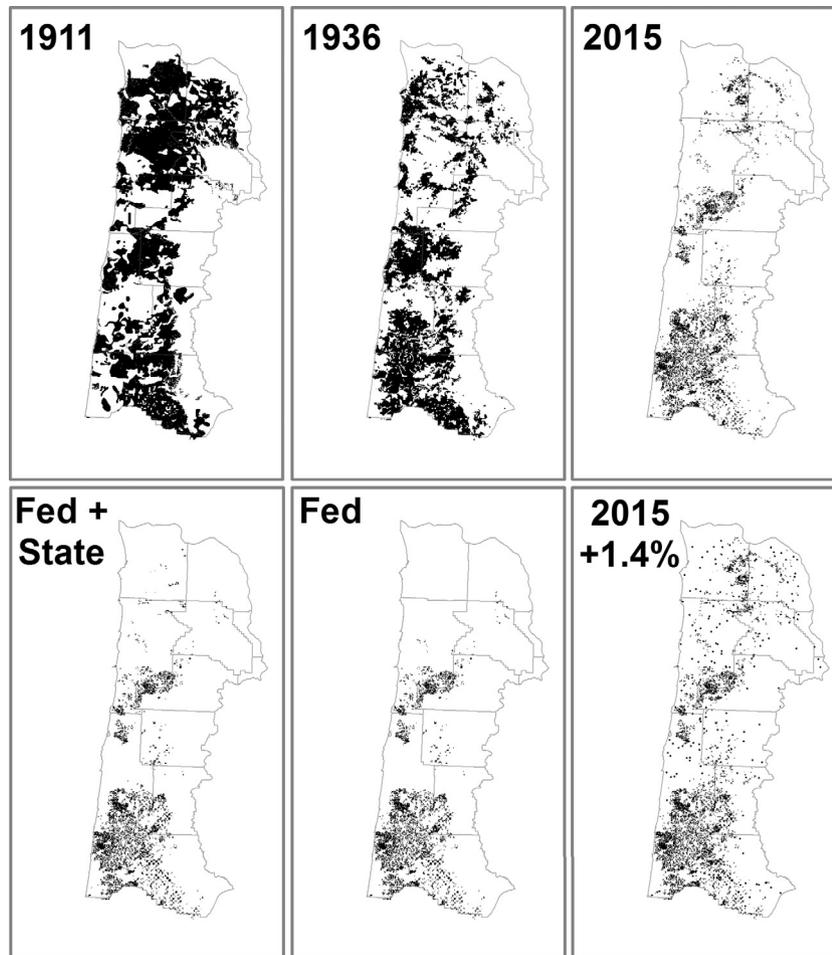


Fig. 6. Comparison of old forest cover (≥ 80 years old) in three landscapes in 1911, 1936, and 2015, two old forest management area scenarios in 2015, and two restoration scenarios in the northern half of the Oregon Coast Range, USA. Old forest management areas were managed to maintain old forest conditions on federal and state lands (Fed + State) and only federal lands (Fed). We show one restoration scenario (2015 + 1.4%) which was simulated by randomly increasing the number of patches in an amount equal to the percentage of old forest lost if old forest contracted to federal lands managed for old forest.

forest may provide habitat for multiple vertebrate and invertebrate species, and provide ecological characteristics that facilitate recolonization (Hunter and Bond, 2001; Mazurek and Zielinski, 2004). Therefore, retention of remnant trees should facilitate more rapid population recovery post-disturbance in low-contrast matrix (Lindenmayer and Laurance, 2016). Landscape context likely matters for emigration but remnant trees may increase suitability of young forest by reducing matrix contrast.

Conservation of existing tree vole populations, in the near term, clearly depends on conservation of remaining old forest, but long-term persistence of tree voles likely depends on what occurs in

what is now young forest. Absent old forest on non-federal lands, we estimated an approximately threefold increase in distances from >20 ha patches of old forest. Alternatively, we provided an example of restoration whereby random placement of additional patches equivalent to a 1.4% increase in old forest within the study area reduced mean distance from nearest old forest patch from an average of 3.1 km (current) to an average of 1.8 km (restoration scenario). Most of our randomly generated additions of old forest occurred on private lands due to prevalence of private lands in our study area, and therefore conservation plans for tree voles would likely be enhanced with a multi-ownership approach

(Andrén, 1994; Burkey, 1989; McAlpine et al., 2007; Ohmann et al., 2007).

Although our restoration example was relatively simple, it demonstrates the potential of even a small amount of additional old forest to provide linkages within forested matrix (Franklin, 1993) for tree voles and potentially other low vagile species that can persist in dispersed patches and that depend on old forest. Restoration may be particularly important because large wildfires that can eliminate large blocks of suitable habitat are predicted to become more frequent and may be more likely to eliminate large reserves of old forest on federal lands (Davis et al., 2017). Conservation and restoration of old forest patches outside of large blocks on federal lands could: (1) reduce distances that emigrating individuals would need to travel before encountering suitable habitat, and (2) reduce the risk that large fires further isolate portions of the study area to the degree that tree voles are unlikely to recolonize. Although we assumed >20 ha patch of old forest could support a population of 1.0–1.9 tree voles per ha, we suggest that future research identify patches of old forest across ownerships that minimize isolation within the study area, followed by field surveys for tree voles to confirm whether such patches and intervening young forest are occupied and could actually function as linkages.

Individual trees and density of large trees can be detected with airborne LiDAR data (Kramer et al., 2016; Wing et al., 2015); however, fine-scale structural characteristics that may limit tree vole occurrence are undetectable. For example, airborne LiDAR data cannot identify complex branch and bole structures of individual trees that tree voles can build their nests on and that may be a limiting factor for tree vole occurrence, especially in intensively managed young forest (Maser, 1966; Swingle, 2005). Our approach at the landscape scale was only able to detect potential habitat based on LiDAR-measured tree height that is well-correlated with forest age and structural development of complex branch and bole structures used by wildlife (Banks et al., 2013; Spies and Franklin, 1991) but lacked resolution at the finest scales to actually detect these structures. We predict that realized habitat for tree voles, especially in young forests, is likely to occur at multiple spatial and temporal scales: very fine, (i.e., individual tree attributes; Swingle, 2005), local (forest cover encompassing ≥ 1 home ranges of tree voles), landscape context (proximity to >20 ha patches of old forest that harbor tree vole populations), time since disturbance, and time to recolonization post-disturbance. We and others that primarily applied local-scale data for tree vole habitat models (Dunk and Hawley, 2009; Johnston and Moskal, 2017) may be missing critical scales for the tree vole, particularly fine-scale structure of trees.

Our model predicted areas with high relative habitat suitability north of the Nestucca River, where tree voles were rare to absent (Fig. 5a; Forsman et al., 2016; Price et al., 2015). If substantial forest loss due to wildfires and timber harvest in the past century eliminated and continues to limit recolonization of recovering habitat (Forsman et al., 2016), then suitable habitat in this portion of the historical range of the tree vole may be most appropriately interpreted as sites suitable for aided dispersal through reintroductions (Pearce and Lindenmayer, 1998). Alternatively, unoccupied suitable habitat may simply have reached the minimum height threshold used to identify old forest in our model, but trees may lack complex structures that serve as suitable foundations upon which tree voles can build their nests. We caution that our selection of >80 years as a threshold may have obscured the contribution of old-growth forest (>200 years old, Spies and Franklin, 1991), which may support the highest densities of structures that tree voles and other arboreal species can use to build their nests on (Banks et al., 2013; Forsman et al., 2016; Swingle, 2005). For a high risk conservation strategy, such as reintroduction (Pearce

and Lindenmayer, 1998), we suggest that field surveys to quantify trees which have structures for nest building be used to complement predicted habitat suitability models prior to considering such a reintroduction.

5. Conclusions

Increasingly, species must adapt to novel landscapes at the pace of landscape-scale change. We identified several important mechanisms that could contribute to conservation planning. For tree voles, young forest may complement overall habitat suitability but this effect is limited to young forest near old forest. There remains uncertainty in the suitability of young forest matrix in providing habitat for emigrants or in the facilitation of demographic and gene flow between more stable tree vole populations that occur in patches or blocks of old forest.

Within the study area south of the Nestucca River, protection of dispersed patches of old forest may complement current moderate- to large-reserves on federal lands by increasing resiliency of tree vole populations by decreasing the risk that large wildfires would eliminate large areas of highly suitable habitat. North of the Nestucca River, the absence of large old forest management areas and distance to nearest tree vole population, may continue to limit recolonization of suitable habitat by tree voles (Forsman et al., 2016). The next step in conservation planning for tree voles in our study area may be to identify remaining patches of old forest within low-contrast young forest matrix that may serve disproportionately to maintain connecting habitat within the current system of old forest management areas and to consider set-asides where young forest is allowed to mature to old forest. The most effective conservation strategy for tree voles will likely include conservation of remaining old forest (Fahrig, 2001), extending conservation outward from remaining habitat, and identifying areas where additional patches of old forest would contribute most to decreasing distances from patches of old forest.

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