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Timber harvest and wildfires drive long-term habitat dynamics for an arboreal rodent

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ABSTRACT

Animals dependent on old, closed-canopy forests may be particularly sensitive to forest disturbances, such as timber harvest and high-severity fires, that may take centuries to recover from. Tracking habitat trends can provide broader context to conservation decisions, including the role of forest disturbance type. We assessed habitat dynamics across the range of the red tree vole (*Arborimus longicaudus*), a canopy-obligate rodent with low-mobility that typically occurs in old forests. We developed and applied a red tree vole habitat model to imagery data each year across 37 years (1986–2022). We quantified changes in habitat across four regions that differed by land ownership and dominant disturbance type. Overall, habitat declined 18 % since implementation of a major conservation initiative (1994–2022). Habitat change was highest in the northern coast (65 %) where timber harvest was the most common disturbance. Within interior regions, several large wildfires in the previous two decades correlated with a 15 % decline of habitat on federal lands, particularly at the northern range periphery where tree voles were already scarce due to historic disturbances. Recruitment of old forest and subsequent recolonization by red tree voles and other low mobility species after high-severity disturbance can take centuries whereas old forest loss can happen rapidly. Given their strong association with old forest, scarcity within historic disturbance footprints, and relatively limited geographic range, we anticipate red tree voles will remain a species of conservation concern.

1. Introduction

Intact forests with large old trees support critical ecological processes but are in precipitous decline globally (Lindenmayer et al., 2012; Watson et al., 2018). Assessing trends in old forest habitats at broad spatial (e.g. landscape-scale) and long temporal extents can provide insights into factors, including forest management and other disturbances, influencing occurrence of old-forest dependent species through time (Lesmeister et al., 2021; Reilly et al., 2017; Spies et al., 2019). Forest loss can happen quickly whereas recruitment of old forest occurs over long time periods, often centuries. This temporal mismatch of rapid habitat loss and slow habitat recruitment may particularly affect highly-mobile animals that require extensive, connected old forests or low-mobility animals that cannot move far to track shifts in old forest cover (Forsman et al., 1984; Linnell and Lesmeister, 2019).

The red tree vole (*Arborimus longicaudus*; henceforth, tree vole) is a small, low-mobility, canopy-obligate rodent that is endemic to highly productive moist coniferous forests of the Pacific Northwest, USA (Forsman et al., 2016; Spies et al., 2018a). Tree voles typically forage in dense forest canopies, and build their arboreal nests on branch and bole structural features that develop most reliably in the oldest trees (Pelt and Sillett, 2008). At the landscape-scale, tree voles appear to be scarce or absent from areas that lack old forest cover, and due to limited mobility may be constrained to connected forest landscapes (Forsman et al., 2016; Linnell and Lesmeister, 2019). Of particular and longstanding conservation concern is the northern periphery of their range in the northern Cascades and the northern Coast Range of Oregon where a distinct population segment is a candidate for protection under the US Endangered Species Act (Forsman et al., 2016; Miller et al., 2006; USDI Fish and Wildlife Service, 2011).

Wildfires and timber harvest in the 20th century resulted in major contractions in the distributions of tree voles and the old forests they depend upon (Forsman et al., 2016; Wimberly and Ohmann, 2004). Tree voles remain extirpated or scarce at the northern periphery of their

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range nearly a century after large fires burned hundreds of thousands of hectares during brief periods of extreme drought and fire weather (Forsman et al., 2016; Kemp, 1967; Reilly et al., 2022). The ability of tree voles to recolonize forests recovering after broad-scale disturbances is poorly understood but thought to be restricted by forest fragmentation and their limited mobility (Forsman et al., 2016; Linnell et al., 2017).

Deforestation in the latter half of the twentieth century was rapid and extensive across the region and in part led to development and implementation of the Northwest Forest Plan (NWFP) in 1994. Under the NWFP, federal land management shifted from a focus on harvesting of old-growth forests to conserving mature (80–150 years old) and old-growth (>150 years old) forests (collectively, old forests) in a late-successional reserve-matrix system (Spies et al., 2019; Thomas et al., 2006; USDA Forest Service and USDI Bureau of Land Management, 1994). During federal implementation of the NWFP, non-federal landowners collectively harvested most remaining old-growth forest and intensified timber management, including shortening harvest rotations (Bliss et al., 2010; Oregon Department of Forestry, 2010). The contrasting forest management of reserve-matrix (federal) and intensive forestry (mostly non-federal), often highly interspersed has strongly shaped old forest distribution within contemporary landscapes (Blumm and Wigington, 2013; Kroll et al., 2020).

Species conservation actions are frequently taken using a snapshot in time of habitat conditions. Because conditions can change rapidly, this approach may be insufficient to make well informed decisions that can affect decades of conservation and forest management. In this context, habitat monitoring using remote sensing can provide the basis for iteratively evaluating trends in forest cover to more frequently inform conservation decisions.

Our objective was to produce a time-series of tree vole habitat by developing and applying a habitat suitability model to annually available imagery data. We assessed annual trends in predicted habitat across four regions that varied by forest management and disturbance regime over 37-years, a period that slightly preceded and spanned NWFP implementation on federal lands and ended with several large wildfires. Specifically, we identified patterns and causes of change in predicted habitat extent, connectedness, and quality by region, and across the range of the tree vole.

2. Materials and methods

2.1. Study area

Our study area encompassed the historic distribution of tree voles in Oregon and northern California (55,352 km^2), bounded by the Columbia River (north), Pacific Ocean (west), high-elevation Cascades mountains (east), and the range of the Sonoma tree vole in northern California (south; Fig. 1; Forsman et al., 2016). Most forests were conifer-

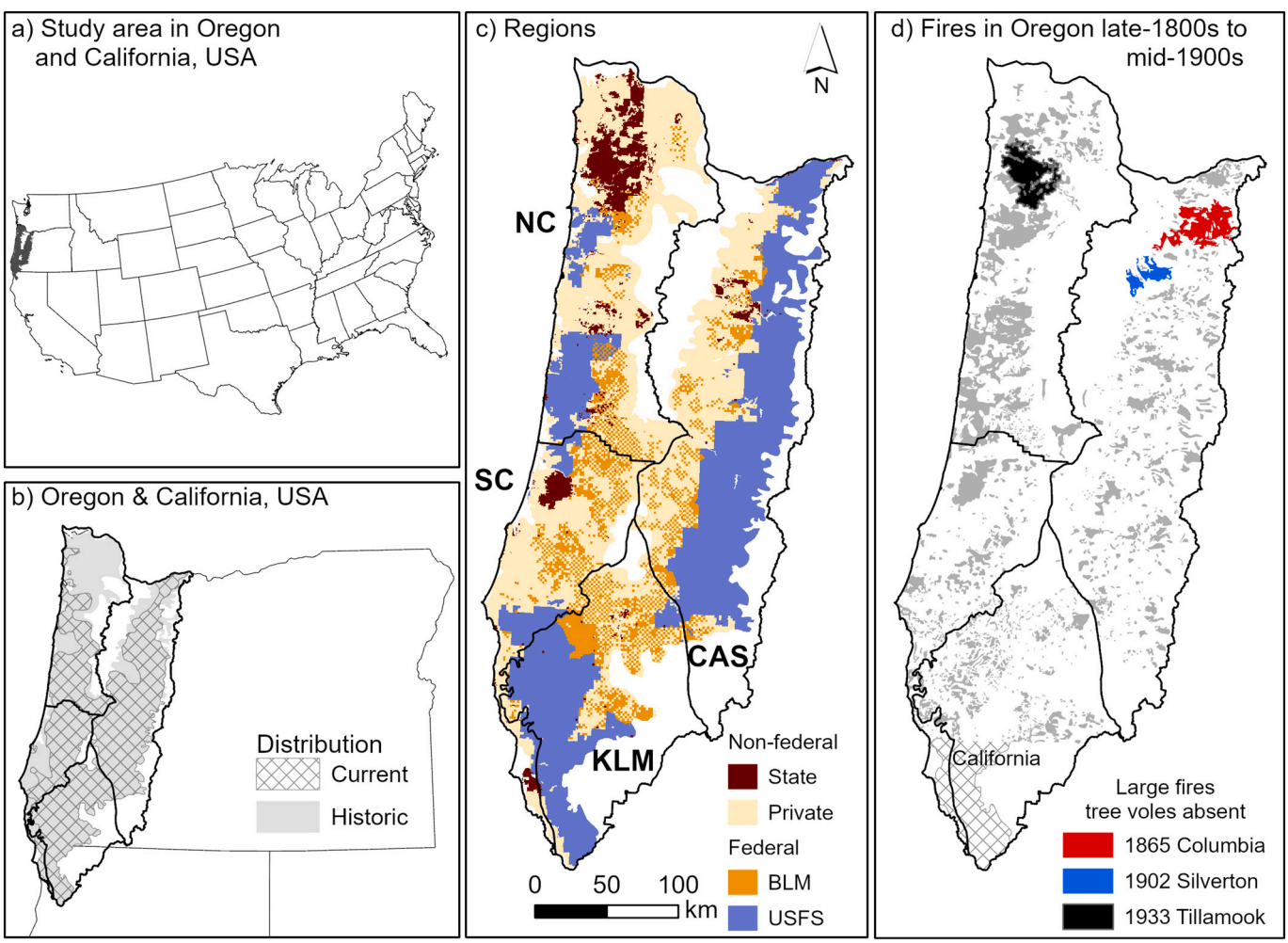

Fig. 1. Current and historic (1914) distribution of red tree voles in Oregon and northern California (panels a, b). Regions and land ownership (panel c) were used to summarize trends. Within the historic distribution, extent of federal land ownership and forest extent varied by region: North Coast (NC; total forest extent = 15,085.3 km^2; 28.2 % federal forest extent), Cascades (CAS; 19,746 km^2; 66.5 %), South Coast (SC; 9330.8 km^2; 34.5 %), Klamath (KLM; 11,189.3 km^2; 73.4 %). Panel d depicts historic fires late-1800s to mid-1900s in Oregon, including where red tree voles remain absent (Forsman et al., 2016).

dominated with hardwoods primarily restricted to rivers and valleys. Tree voles use several widespread conifer species for foraging and nesting ("forage trees"): Douglas-fir (*Pseudotsuga menziesii*) were well distributed across the study area, western hemlock (*Tsuga heterophylla*) more common in northern interior and coastal forests, and Sitka spruce (*Picea sitchensis*) limited to near-coast forests (Forsman et al., 2016). These trees primarily occurred from sea-level to seasonal snowline.

Forest type (moist or dry), disturbance regime, and land ownership varied broadly across regions (Spies et al., 2018a; Zald and Dunn, 2018). Historically, fire frequency generally decreased with increasing latitude and proximity to the Pacific Ocean (Spies et al., 2018a). In moist coastal and northern interior forests, destructive large wildfires were historically infrequent with return intervals of several centuries (Spies et al., 2018a). Early forest mapping efforts noted that the Oregon Coast Range

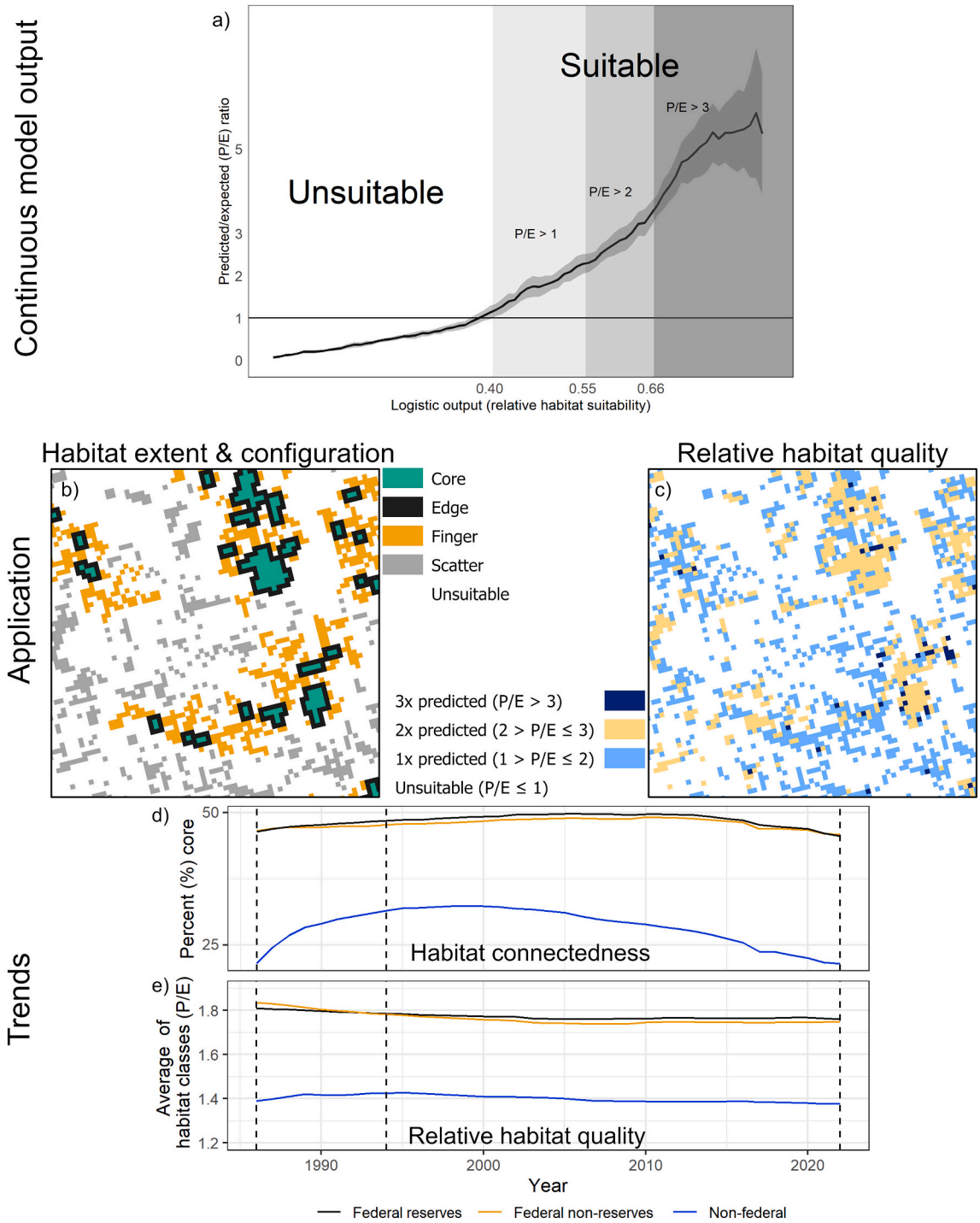

Fig. 2. Assessing habitat configuration and quality. We used the predicted to expected ratio curve and continuous model output (Panel a) to assess habitat configuration (binary suitable/unsuitable 1/0; Panel b) and relative habitat suitability (Panel c). Core pixels were any suitable pixel surrounded on all 8 sides by other suitable pixels (Panel b). Habitat quality indexed the number of red tree vole nests predicted at each pixel relative to expected by chance, e.g. at $P = 2$, twice as many nest locations would be predicted to occur relative to $P/E = 1$. We binned suitable pixels into 3-classes (1,2,3) using the lower end of the P/E curve value, e.g. all values in the range $2 > P/E \leq 3$ were binned as having value 2. Panel e is the average of these three classes. We show example trends across land-ownership and reserve land-use allocations (Panel e).

and northern half of the Cascades had incurred extensive burns where "the destruction of timber was nearly or quite complete" (Gannett 1902).

High severity fires and subsequent salvage logging eliminated nearly all old-growth trees in the burn footprints of the Columbia (1865), Silverton (1902), and Tillamook fires (1933–1951) – tree voles remain absent within these fire footprints (Fig. 1; Forsman et al., 2016; Kemp, 1967). As noted in early mapping efforts, the southern portions of the Coast Range and the Cascades had widespread signs of fire, but "destructive fires" were few and small (Gannett 1902). Forests of the Klamath and southern Cascades typically experienced mixed-severity fires occurring at moderate frequency (50–200-year interval) over smaller areas (Agee, 1993; Spies et al., 2018a). Interior (Cascades, Klamath) and coastal (North Coast, South Coast) regions were broadly similar to each other and for some comparisons we summarized them together. Each region contained >9000 km^2 of forests within the footprint of the historic distribution of tree voles (Fig. 1).

The NWFP established a network of late-successional reserves where the management focus was maintenance and restoration of old forest (Spies et al., 2019; USDA Forest Service and USDI Bureau of Land Management, 1994). Conservation for late-successional and old-growth forests within the NWFP areas occurred almost exclusively on federal lands (Spies et al., 2019; Thomas et al., 2006). In 2016, the Bureau of Land Management (BLM) established two Resource Management Plans for Oregon which superseded the NWFP on BLM lands within the range of the tree vole but maintained many of the same standards and guidelines of the NWFP (USDI Bureau of Land Management, 2016a, 2016b). The US Forest Service continued to implement the NWFP throughout the duration of the study. In our analyses, we used the reserve land-use allocations as designated by plans of the respective federal agency.

Federal forests comprised 52.1 % of total forests and non-federal the remainder: private (41.6 %), state (5.8 %), and all other (<1 %). Most non-federal forests were managed intensively for timber production as plantations of native conifers (primarily Douglas-fir) on 40–80 year rotations (Adams et al., 2002; Oregon Department of Forestry, 2010).

2.2. Developing and applying a red tree vole habitat model

Tree vole habitat comprises trees suitable for foraging and nest-building, and connected forest landscapes containing many suitable trees that support a population. We created a tree vole habitat model at 30 m resolution (900 m^2 pixels) – a resolution that conformed to spatial area requirements of individuals (median home range size = 760 m^2; Swingle and Forsman, 2009), and to GIS layers used as model covariates. The first step in our modeling process was to produce a habitat model using presence-only location data that represented conditions across our study area. We then applied our habitat model algorithm to annual imagery to produce a time-series. We used our final habitat model to assess trends in habitat quality and connectedness through time and across regions, disturbance regime, and land ownership (Fig. 2).

We trained and tested our model using presences – spatial locations where one or several tree vole nests were found during surveys conducted 1995–2019. Surveys consisted of ground-based visual searches to locate tree vole nests in the canopy followed by tree-climbing to confirm presence of tree vole sign (Lesmeister and Swingle, 2017). We eliminated presences that occurred in forests disturbed (i.e., canopy cover reduced to <60 %) prior to 2017, the year in which GIS layers used in our model were produced (Huff, 2016).

Sampling effort was uneven across regions – in some areas sampling was intensive resulting in many clustered locations whereas other areas sampling was sparse. To ensure presences represented conditions where tree voles occurred across regions, we thinned, and scaled our data by region. First, we thinned our data, keeping one random location per 1-km (Aiello-Lammens et al., 2015). Second, we scaled presences such that the ratio of locations to area was equal within each region. We assumed presences represented conditions where tree voles occurred across our study area, and therefore interpreted model output as relative habitat suitability (Merow et al., 2013; Royle et al., 2012).

We used our presence-only data to train and test a tree vole habitat model in Maxent (version 3.4; Phillips et al., 2006). Briefly, Maxent uses a deterministic mathematical algorithm to maximize the entropy (a measure of dispersedness) between presences and a random sample representing background conditions across covariate space (Elith et al., 2011). Maxent applies multiple transformations to each covariate (e.g. fits a quadratic function) to more closely fit distribution of presences to covariates. Transformations have the additional utility of representing the often complex and frequently non-linear relationships of the environmental niche space that species occupy. Model output from Maxent ranks relative density whereby higher density falls closer to the mean of the distribution of transformed covariates. We used linear, product, and quadratic transformations on nine covariates that we selected based on known species-environment relationships (Table 1; Forsman et al., 2016; Merow et al., 2014).

Model covariates were broadly categorized as forest structure, tree species composition, and abiotic. We only considered forests as potential habitat, i.e. lands that had current or previous evidence of forests and that had not been converted to other uses, such as agriculture. We masked out non-forests following conventions used to create forest covariates (Bell et al., 2021).

Forest structure and tree composition were based on gradient nearest

Table 1
Description of covariates used in red tree vole range-wide suitability model. Forest structure and tree composition were developed using gradient nearest neighbor techniques whereas abiotic were interpolated from coarse resolution (800 m) temperature and climate data (PRISM). We evaluated individual covariate performance across 10 bootstrapped model runs as the ratio (percentage %; mean ± 1 standard deviation) of single-covariate model training gain relative to the full model. Higher values indicate strong performance relative to full model.

Covariate	Description	Accuracy[a]	Covariate type	Performance relative to full model
Conifer cover	Percentage cover of conifers	0.79	Forest composition	39.8 ± 3 %
Density of large conifers	Density (trees per ha) of trees > 75 cm dbh	0.67	Forest structure	38.4 ± 3 %
Diameter diversity index	Weighted diversity of tree diameters; higher weight assigned to largest trees	0.74	Forest structure	48.0 ± 2.5 %
Hardwood cover	Percentage cover of hardwoods	0.69	Forest composition	4.9 ± 1.8 %
Forage (food) trees	Basal area of forage trees[a]	0.70	Forest composition	41.6 ± 3.5 %
Non-forage trees[c]	Basal area of non-forage trees[b]	0.37	Forest composition	11.7 ± 2.1 %
Precipitation	Average annual precipitation	n/a	Abiotic	5.1 ± 1.1 %
Summer fog	Index of summer fog	n/a	Abiotic	20.5 ± 2.2 %
Temperature	Average maximum temperature in August	n/a	Abiotic	9.3 ± 1.8 %

[a] Pearson's correlations for Gradient Nearest Neighbor interpolation from forest inventory vegetation plot data across GNN model regions within our study area. Accuracy reports were not available for Abiotic covariates.

[b] Forage trees were Douglas-fir and Sitka spruce. Although tree voles forage in western hemlocks in near-coast forests, inclusion would over-represent forage trees where western hemlocks are abundant such as the Cascades.

[c] Non-forage trees were an aggregate of tree species: coast redwoods, pine, subalpine fir, and white fir.

neighbor (GNN) imputation. GNN incorporates Landsat satellite imagery, climatic and topographic data, and USDA Forest Inventory and Analysis (FIA) to predict forest covariates (Bell et al., 2021). Landsat and GNN covariates rely on light reflecting from the canopy. Shadowing caused by partial canopy cover can cause erroneous readings that affect old-forest covariates. Greatest uncertainty occurred in older forests where timber harvest removed partial canopy – thinning, a widespread harvest management method used on federal lands (Davis et al., 2022).

Accuracy assessments indicated relatively high performance of most GNN model covariates (Pearson correlation coefficients (r) $\geq$ 0.67; Table 1; Bell et al., 2015). GNN data were produced at 30 m resolution each year by the Landscape Ecology Modeling, Mapping & Analysis group (https://lemmadownload.forestry.oregonstate.edu/). Annual GNN layers were produced at the beginning of a model year, and therefore annual differences (e.g. forest loss) occurring in year x would first be detected in model year x + 1.

We used performance metrics (training and testing gain, area-under-the-curve, continuous Boyce index) to assess how well our model distinguished presences from non-presences in testing data (Boyce et al., 2002; Hirzel et al., 2006; Linnell et al., 2017). We used training gain to evaluate our full model (all covariates) and performance of individual-covariate models relative to our full model (Table 1). To ensure we did not over-fit our model by applying excessive transformations to covariates resulting in a model that did not generalize well across our study area we applied regularization multipliers (0.5 to 3.0 at an interval of 0.5) whereby higher regularization multipliers penalized more complex models (Elith et al., 2011; Merow et al., 2013; Phillips and Dudík, 2008). We selected the highest regularization multiplier where the model retained high performance. We used the predicted to expected ratio curve (P/E ratio curve) of the continuous Boyce index to evaluate model performance. A good model should have a monotonously increasing P/E curve. We produced a P/E ratio curve (mean and 95 % confidence interval) by running 10 iterations of our final habitat model (Fig. 2).

The P/E ratio curve increases with higher predicted suitability and we used this relationship to identify breaks in continuous model output where habitat occurred and was of higher quality (Hirzel et al., 2006; Soille and Vogt, 2009). We classified suitable (habitat) where the model predicted >1 presence (tree vole nest) would occur relative to chance (P/E > 1; Fig. 2). We used a binary suitable/unsuitable (1/0) layer to assess habitat configuration; specifically, we identified connectedness using core pixels, whereby core pixels were defined as suitable pixels where all eight neighbors were also suitable (Soille and Vogt, 2009). We used the percentage of core pixels as an index of habitat connectedness whereby a higher percentage indicated greater habitat connectedness (Fig. 2d). To assess relative habitat quality at each pixel, we subdivided habitat (P/E > 1) into three classes (Fig. 2a). Habitat quality was principally independent of habitat configuration and extent as it indexed only habitat pixels regardless of extent (Hirzel et al., 2006; Fig. 2).

We used Google Earth Engine to apply our habitat model algorithm (Maxent lambda files) to annual GNN layers for years 1986–2017 (Gorelick et al., 2017). GNN layers were not available 2018–2022. To document trends in forest loss during those years, we used a remotely-sensed multispectral index called the normalized burn ratio (NBR) layer to identify where tree canopy cover was reduced to <40 %. The NBR is widely used to map forest disturbance effects such as wildfire by differencing pre- and post-disturbance NBRs (Miller et al., 2009). However, NBR by itself is highly correlated with live tree canopy cover (Lesmeister et al. 2019; Fig. 3; https://timesync.forestry.oregonstate.edu/storages/arlo/) which is an important component of tree vole habitat. Thus, where NBR was below 0.4 at the end of the calendar year, canopy cover was considered to be <60 %, a threshold associated with "non-habitat" (Huff, 2016) and we re-classed pixels as non-habitat.

Abiotic covariates (Table 1) were averaged across 30-years (30-year normal; 1991–2020; https://prism.oregonstate.edu/) and we set these as constant through our time-series. We used bilinear interpolation to resample the 800 m resolution of abiotic covariates to 30 m resolution to match our GNN layers.

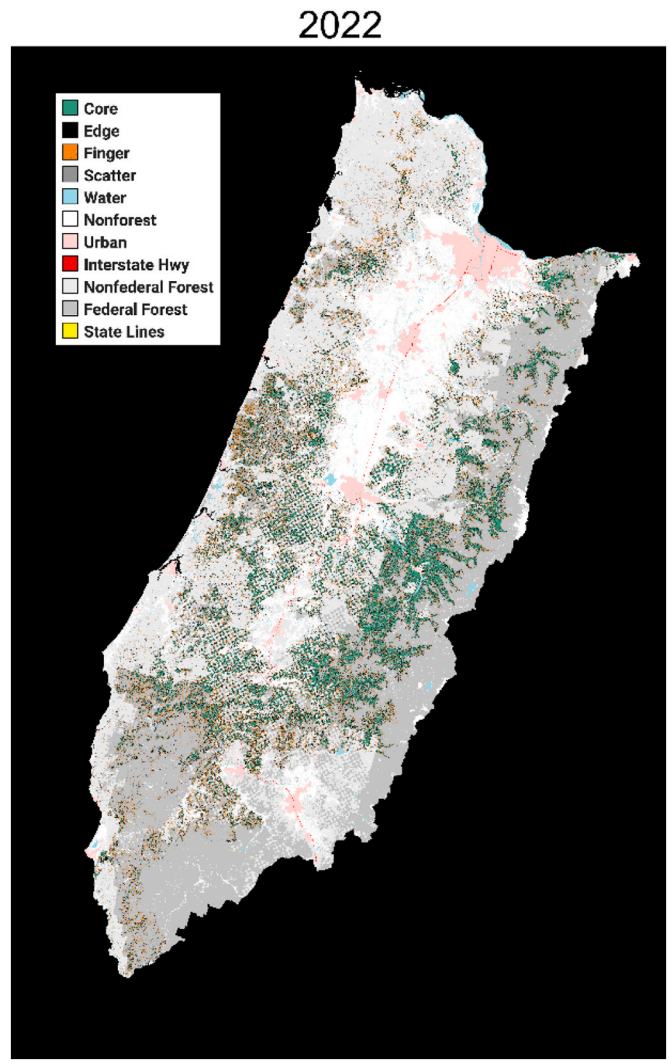

Fig. 3. Trends in red tree vole predicted habitat over 35-years (https://timesync.forestry.oregonstate.edu/storages/arlo/). Shown are connected core habitat (green, black) and habitat containing no core but connected by a chain of one or more pixels to core (orange).

We quantified extent of connected habitat (core), and disturbance leading to habitat loss by region, ownership (federal, non-federal), and reserve status (reserve, non-reserve). We used maps of fire perimeters (https://www.mtbs.gov/) to identify where habitat loss was attributable to fires. We assumed habitat loss outside of fire perimeters was primarily from timber harvest as we estimated forest loss from other disturbances, e.g. insects and disease were < 1 % and typically low-severity https://www.fs.fed.us/foresthealth/applied-sciences/mapping-reporting/detection-surveys.shtml).

3. Results

We started with 1799 presences that we thinned to 1672, a minimum of 1 km from the nearest neighboring presence. The North Coast modeling region had the lowest ratio of presences to area ($n = 256$ for 15,085 km^2 of forest; 1 presence per 59 km^2), and we used this ratio to scale presences for other regions. We used 1096 presences in our final model.

Our habitat model used a regularization multiplier of 1.0 and performed relatively well. We estimated a continuous Boyce index of 0.98

± 0.02 (mean ± 1 standard deviation) and area-under-the-curve of 0.79 ± 0.01. Our threshold for suitable was >0.40 (Fig. 2). Forest structure, canopy cover, and forage trees performed better, relative to the full habitat model, than abiotic covariates (Table 1).

Habitat extent on non-federal lands peaked in 1998, three years after implementation of the NWFP, and declined 60 % 1998 to present. After increasing 19 % (reserves) and 23 % (non-reserves) in the period 1986 to 2013, habitat extent peaked, and then declined on federal lands. By the end of our time-series (2022), habitat extent remained constant (<1 % gain) or increased slightly (6 %) 1986 to 2022 on federal reserves and non-reserves, respectively.

These increases were not consistent across the time-series. Since implementation of the NWFP in 1994, habitat extent decreased 8 % in reserves; non-reserves increased 1 %. Habitat quality, defined as the average value of habitat pixels after classifying into 3 P/E classes, was highest at the beginning of our time-series but decreased steadily by 3 % and 5 % on reserves and non-reserves, respectively (Fig. 2). This

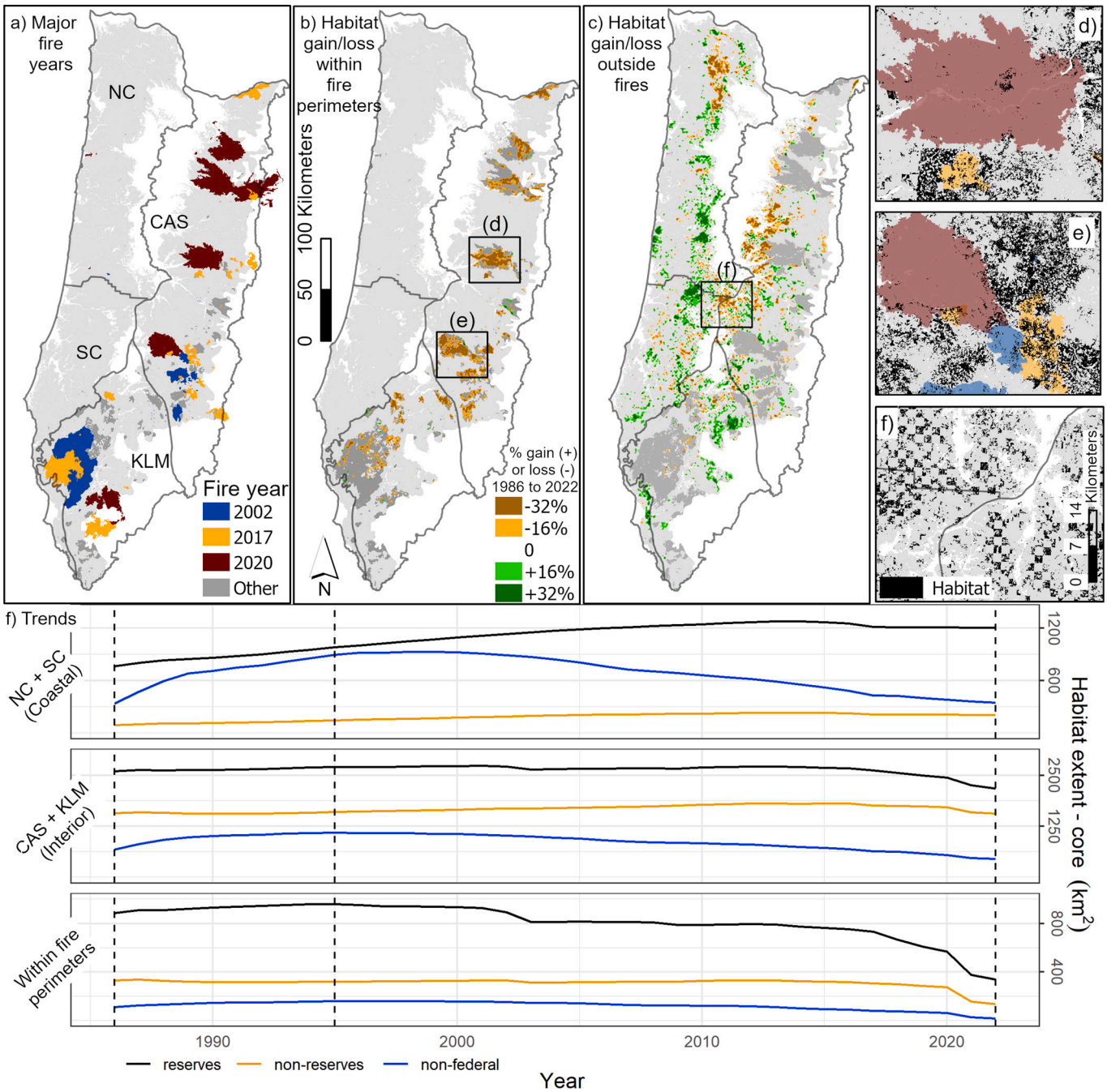

Fig. 4. Summary of % habitat gain or loss attributable to fires and timber harvest across regions (1986–2022). We used the distribution of change in habitat extent across the historical distribution of red tree voles to identify 1 (16 %) or 2 (32 %) standard deviations from no change (0 %). Panel a shows the pattern of fire by year across regions. Panels b and c show loss attributable to fires and other disturbances (timber harvest), respectively, and gains due to forest recruitment (panel c). Panel d shows the fire perimeter of the 2020 Holiday Farm fire in the Oregon Cascades. Panel e shows examples of high-severity (2020 Archer Creek fire) where virtually no habitat remained post-fire, and mixed-severity fires in 2002 (Apple fire) and 2017 (Happy Dog, North Umpqua fires) where some habitat remained post-fire (mtbs.gov). Panel f shows extensive loss of habitat within a transition zone between tree regions. Vertical dashed line indicates implementation of the Northwest Forest Plan on federal lands.

decrease, particularly on federal lands, did not appear correlated with habitat extent (Fig. 2d, e). Habitat connectedness (% of habitat as core) had an overall decrease of 12 % and 8 % since implementation of the NWFP, on federal reserves and non-reserves, respectively (Fig. 2d).

Losses and gains in habitat extent were not evenly distributed across regions or land ownerships. Trends in habitat extent on federal lands were nearly identical in coastal regions, and generally increased in reserves and non-reserves. On non-federal lands, after peaking in 1998, extent decreased 68 % and 52 % in the North and South Coast, respectively (Fig. 3). In the Cascades and Klamath, habitat extent on federal reserves showed distinct decreases after large fires in 2002, 2017, and 2020 (Fig. 4). Non-federal forests in most regions peaked between 1995 and 2000 except for the Klamath region.

Of the total 2480.4 km^2 habitat lost across regions, 55.9 % was located within fire perimeters and 45.1 % within non-fire disturbances, principally timber harvest (Fig. 4). Overall change (% habitat gain + % habitat loss pre- and post-peak) was greatest in the North Coast at 65 % followed by the South Coast (42.3 %), Klamath (34.8 %), and Cascades (27.6 %). Fires were not extensive in the coastal regions (<1 %) and therefore, change in habitat was attributable to timber harvest. By contrast, within the Klamath and Cascades regions, 32.5 % and 23.2 % of habitat loss occurred in forests within fire perimeters.

Extent of habitat retained within fire perimeters broadly varied by fire regime: almost no habitat was retained within 2020 fire perimeters (Fig. 4 d). Although we note some habitat was retained at the eastern flank of the Archie Creek fire (Fig. 4e), perhaps due to strong winds from the east that pushed the fire westwards downslope of its ignition source. In previous years (2002, 2017), we show where fires adjacent to 2020 fires burned at mixed-severity (mtbs.gov; Fig. 4e).

4. Discussion

Effective conservation depends on reliable prediction of current and future habitat conditions. We identified habitat change for an old-forest dependent species over a 37-year period that provided insights into trends of quality and configuration of habitat. Where tree voles were of greatest conservation concern in the North Coast, habitat extent steadily declined on non-federal lands in the previous two decades, and loss was consistent with timber harvest. Within interior regions, wildfires, including recent fires that occurred during extreme drought and fire weather coincided with rapid reduction in habitat extent across land ownerships, particularly in the northern Cascades where tree voles were already scarce, increasing conservation concern there. These patterns provide insights into contemporary processes that shape habitat, and we discuss potential clues into future habitat loss and recruitment.

We identified uncertainty in disturbance severity that could affect interpretation of model output. First, when continuous model output values were near the suitable/non-suitable threshold, individual pixels could oscillate 1/0 for a period of time due to small variations in imagery data that are sensitive to this threshold. Next, imagery used in forest structure and composition covariates can misclassify forest canopy-loss from thinning as canopy-gain resulting in over-estimation of habitat gains across the 10,000 s of acres of old forests thinned annually on federal lands within the NWFP (Davis et al., 2022; Spies et al., 2018b). Therefore, tree vole habitat models could be improved with detailed measures of disturbance severity and type, particularly if habitat models are used to inform management (Davis et al., 2022).

Amplitude and consistency of habitat change varied across forest management systems. Habitat extent on non-federal lands peaked just after implementation of the NWFP, followed by steady decreases in habitat extent, quality, and connectedness. If intensive timber production (shorter harvest rotations) remains prevalent on non-federal lands, we expect trends of short-term habitat gain followed by loss to continue. Trends on federal lands followed patterns typical of an infrequent fire regime – long periods of habitat stability or recruitment punctuated by sharp drops in habitat extent driven by high-severity disturbances. Overall, habitat appears to have broadly contracted to federal lands during our time-series. Where federal lands are isolated, broad contraction to the federal lands footprint could increase the risk that one or several stochastic events such as large fires eliminate or isolate populations (Linnell et al., 2017).

We quantified abrupt habitat loss due to recent large fires leading to extensive barriers that are likely to isolate tree vole populations for centuries to come. Driven by strong, drying east winds the 2020 wildfires burned a nearly continuous east-west forest break across several lower elevation forests where tree voles reside (Evers et al., 2022; Reilly et al., 2022). As fires pushed downslope from the east, nearly all tree vole habitat was burned at lower elevations. This pattern is consistent with historic and pre-historic large fires that have occurred each century for the past three centuries in the Oregon Cascades and North Coast, where 'fire winds' led to near-total loss of old forests across extensive areas (Forsman et al., 2016; Kemp, 1967; Munger, 1944). The 2020 Riverside fire burned adjacent to 1865 and 1902 wildfires and where tree voles remain absent, further isolating the northernmost interior stronghold in the Columbia River Gorge where most habitat burned in 2017 (Figs. 1, 4; Forsman et al., 2016). Although some forests have regenerated, tree voles and their habitat remain absent or scarce from their northern periphery nearly a century after fires (Forsman et al., 2016; Price et al., 2015).

Scarcity of tree voles at their northern periphery is almost certainly not entirely due to lack of contemporary habitat. Processes occurring across different return intervals: climate change (10s to 10,000 s of years), wildfires (100 s of years), and timber harvest (10s of years) have all potentially contributed to contemporary scarcity (Forsman et al., 2016; Linnell et al., 2017; Miller et al., 2006). For example, tree voles at their northern periphery contained genetic signatures (haplotypes) distinct from each other (coastal v. interior) and from the southern portion of their range, consistent with forest fragmentation in the north during recent glaciation (circa 12,000 years ago; Miller et al., 2006). As glaciers receded, tree vole populations appear to have slowly recolonized from refugia that contained *Pseudotsuga* or other forage trees (Bonnicksen, 2000). More recently, wildfires have isolated some populations in both interior and coastal regions (Forsman et al., 2016). Slow recolonization, including across deeper time, has shaped occurrence and genetics of tree voles, most notably at the northern periphery.

As forests across their range enter a warming period, forest fragmentation including shifts in composition and structure accelerated by wildfires are predicted to be greatest at the southern periphery (Davis et al., 2017; Halofsky et al., 2020; Tepley et al., 2017). Northern forests, particularly along the coast, are predicted to remain cooler and moister as warmer and drier climate pushes northward in the coming decades and centuries (Davis et al., 2017). Paradoxically, at the northern periphery, conversion of many wetter and cooler coastal forests to intensive forestry, and the continued scarcity or absence of tree voles appears to have rendered many of these forests least capable of supporting tree vole populations as climate warming pushes northward.

Forest refugia containing tree voles and their habitat can form through processes at multiple spatial and temporal scales. As climate warms, near-coast forests that remain wetter and cooler could provide refugia, although federal lands are relatively less extensive in coastal regions. Alternatively, disturbances that create resiliency could form refugia for tree voles and their habitat. Within the mixed-severity fire regime old-growth forests are relatively more resilient and tree vole habitat can remain within fire perimeters (Fig. 4e; Lesmeister et al., 2021; Reilly et al., 2017; Zald and Dunn, 2018). Maintaining or recruiting even a small amount of habitat post-disturbance can reduce dispersal distances between remnant habitat if tree voles remain post-disturbance (Linnell et al., 2017). Extensive tree vole habitat coincides with the mixed-severity fire regime in the Cascades. It remains unknown if scattered old forest can support long-term stability of tree vole populations within interior regions, but could be informed by better understanding whether tree voles and their habitat remain post-fire.

A particular strength of habitat trends across a time-series is the capacity to adapt conservation decisions based on ongoing trends. For example, a decision about providing Endangered Species Act protections for the North Coast distinct population segment will likely be informed by habitat extent and trends, including updating models produced using older remote-sensing data from 2006 (Forsman et al., 2016) and 2006–2016 (Linnell et al., 2017), respectively. Our modeled habitat trends showed slow habitat increases on federal lands but up to 50 % habitat decrease on non-federal lands since 2006 in the North Coast.

Habitat monitoring provides a valuable tool for conservation as it can be substantially less expensive than population monitoring, and remote sensing tools have become increasingly available. Habitat monitoring, however, should not be considered a standalone research or conservation effort as validation of population responses to habitat change is frequently not possible using remote sensing. Rather, it presents opportunities to assess land cover changes that could profoundly impact populations, such as extensive wildfires that eliminate large blocks of habitat. Thus, habitat monitoring can help focus research questions that address conservation issues by providing baseline patterns of habitat and the processes shaping disturbance and habitat recruitment through time.

CRediT authorship contribution statement

Mark A. Linnell: Conceptualization, Methodology, Validation, Formal analysis, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Damon B. Lesmeister:** Conceptualization, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Zhiqiang Yang:** Software, Formal analysis, Writing – review & editing, Visualization. **Raymond J. Davis:** Conceptualization, Methodology, Validation, Writing – review & editing.

Declaration of competing interest

The authors of this manuscript submission declare no conflict of interest that would bias or otherwise inappropriately influence this manuscript.

Data availability

Data will be made available on request.

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