

CONTRIBUTED PAPER

Characterizing long-term population conditions of the elusive red tree vole with dynamic individual-based modeling

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Abstract

Old growth forests are declining globally, threatening dependent wildlife. Many arboreal old-growth obligates, such as the threatened red tree vole, are difficult to monitor for changes in habitat occupancy, and abundance. Yet, conservation planning relies on this information to prevent population declines. We integrated a range of species, habitat, and landscape change information to develop a dynamic habitat-population model. The spatial individual-based model simulated dynamic patterns of occupancy that responded to annual habitat maps, describing 36 years of observed change. We simulated population dynamics and local movement to characterize changes in occupancy and abundance, and the capacity of remaining habitat to support red tree voles. Red tree vole redistribution patterns strongly corresponded to wildfire footprints and timber extraction locations. Population strongholds are likely to exist in clumped pockets of old-growth forest that were unaffected by wildfire and in protected old forest reserves. However, the exact number and locations of local clusters remain uncertain. Simulated population losses occurred at different paces in different places, underscoring the need for recurring evaluation of population changes with field occupancy surveys and modeled evaluations that can anticipate potential connectivity and extirpation thresholds. This modeling approach was effective at leveraging existing information for a data-light species to assess how historical changes to the quantity, quality, and configuration of habitat likely influenced the potential landscape capacity, species abundance, and distribution. Dynamic individual-based modeling can benefit conservation planning for red tree vole and other reclusive forest species by providing biologically nuanced assessments of abundance and distribution. Such models can also project the long-term benefits and impacts of spatially explicit land management plans.

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KEYWORDS

arboreal mammal, dynamic habitat, dynamic occupancy, HexSim, individual-based model, landscape change, old growth forest

1 | INTRODUCTION

Old growth forests are rapidly declining in many parts of the globe, with implications for resident wildlife. Old forests once covered most of the Coastal Ranges and Cascade Mountains of the Pacific Northwest United States, supporting many wildlife species associated with old growth (Thomas et al., 1993; Marcot et al., 2018). However, in the last half of the 20th century, intensifying timber harvest, wildfire, development, pathogens, aridity, and other changes have drastically reduced old growth cover (Lindenmayer & Laurance, 2017; Reilly et al., 2022). In 1994, the Northwest Forest Plan was developed and implemented on approximately 10 million ha of federally administered lands, to maintain timber supply for local communities as well as protect and restore old forests to sustain biodiversity (Spies et al., 2019). Old forest coverage was maintained on federal lands during 1993–2017 (0.3% net increase), indicating that forest succession expectations in the Northwest Forest Plan compensated for old forest losses from wildfire, timber harvest, and other causes (Davis et al., 2022). However, the overall rate of old growth forest loss is accelerating across land ownerships (e.g., public and private lands; Davis et al., 2022; Lesmeister et al., 2021).

The loss of old trees can be particularly consequential for arboreal species that require complex forest structure for nest building and movement. Tree-dwelling wildlife are particularly vulnerable to changes in forest age and structure, as they live their lives in large trees, moving only short distances on the ground among trees (e.g., Lindenmayer & Lacy, 1995). As such, old forests provide unique environmental conditions and fill ecological roles that cannot be replaced by young trees and forests (Lindenmayer et al., 2012). Forest loss has resulted in habitat loss, degradation, and fragmentation for old-growth obligates in the Pacific Northwest including the northern spotted owl (*Strix occidentalis caurina*) and one of its key prey, the red tree vole, hereafter, “tree vole” (*Arborimus longicaudus*; Forsman et al., 2016; Lesmeister et al., 2018). Wildlife population impacts of spatial and temporal changes in old-growth forests are generally not well understood or quantified (Lindenmayer & Taylor, 2020).

Changes in old forests have occurred unevenly through space and time, and accelerated in many places in recent decades (Strittholt et al., 2006). For example,

stand-replacing wildfires have intensified in the Pacific Northwest (DellaSala & Hanson, 2019), as exemplified by the 2020 megafires in Oregon (Reilly et al., 2022). These large and dynamic landscape changes complicate long-term population assessments for sensitive species. The scale and intensity of changes vary by location, making it difficult to measure or track their impacts on populations. Moreover, it is often impractical to monitor and assess annual changes in habitat suitability, occupancy, and demography for animals that are difficult to detect or that have extensive spatial distributions. Yet, forest and species management plans must still anticipate the scope and trajectory of continued disturbances to plan future environments that support diverse wildlife communities.

Dynamic habitat–population modeling can support the development of management and conservation plans by integrating a range of ecological information to gain an understanding of past or future changes on potential wildlife outcomes. For example, maps of forest composition and structure can be used to characterize incremental habitat changes through space and time, then serve as inputs to spatial population models that integrate habitat changes with dynamic wildlife movement, occurrence, density, and abundance, using available empirical data and uncertainty assessments. Spatially explicit individual-based models (IBMs) are particularly useful for data integration and assessing the impacts of cumulative landscape change on species distribution and persistence (Heinrichs & Marcot, 2019). IBMs can couple timeseries of landscape/habitat maps with population conditions and wildlife responses, to characterize cumulative, long-term changes in population occupancy, movement, dispersion, demography, and persistence. IBMs can be used to identify locations and configurations of habitats likely to remain occupied in changing landscapes (e.g., Bancroft et al., 2016; Nogueira-McRae et al., 2019), to determine the capacity of the remaining habitats to support viable populations (e.g., Heinrichs et al., 2010; Heinrichs, O'Donnell, et al., 2019), to identify local populations likely to become extirpated, and to project which are likely to remain as source strongholds (e.g., Heinrichs, Lawler, et al., 2019). More generally, the results of such approaches can be used to direct monitoring and mapping efforts to better understand habitat change and population responses (Schumaker et al., 2014), and to

plan future landscapes that include sufficient qualities, quantities, and configurations of habitat to support viable populations (Dunk et al., 2019).

In this paper, we evaluate the applicability of this simulation approach for generating ecological insights for the management of a data-limited arboreal species, using the tree vole as a case study. To do so, we constructed a spatially explicit IBM for tree voles across their range. Specifically, we (1) assessed the influences of long-term landscape change on the occupancy, abundance, and population trends of an old-growth forest specialist, (2) examined the influence of key knowledge gaps and parameter uncertainties on simulated population outcomes, and (3) developed a modeling framework that can be extended to forecast the implications of future landscape and habitat changes. In doing so, we provide an example of a simulation model that can inform on plausible population outcomes resulting from decades of multiple and varied habitat changes.

2 | METHODS

Tree voles are tree-dwelling rodents that occupy late successional forests of western Oregon and northern California (Dunk & Hawley, 2009; Figure 1). The older trees in

which they build nests are declining as a result of logging, fire, and development (Forsman et al., 2016). Their use of younger forests (20–80 years old) appears ephemeral and occupancy may depend on colonization from nearby old-forest refugia (Forsman et al., 2016; Linnell et al., 2017). Systematic surveys to locate nests have documented the species' habitat associations and forest occupancy; however, coverage is temporally and spatially incomplete across the species' overall range. Tree voles are difficult to locate and confirm presence of their active tree nests. They often build more than one nest within their home range and accumulate inactive nests in proximity to actively used nests. These factors contribute to uncertain estimates of occupancy, density, abundance, and demography (Forsman et al., 2019).

Red tree voles have been a species of concern for decades, receiving special protection under the Northwest Forest Plan in 1994 (USDA and USDI, 1994; Molina et al., 2006), as well as global recognition as a species of conservation concern by the IUCN (Near Threatened and Declining; IUCN Red List, 2021). A distinct population segment (DPS) of tree voles that inhabits the north Oregon Coast Range (Figure 1) was recognized as imperiled and in need of protection under the US Endangered Species Act (USFWS, 2011). However, a 2019 decision reversed that determination (USFWS, 2019). The U.S. Fish and Wildlife Service was issued an intent to

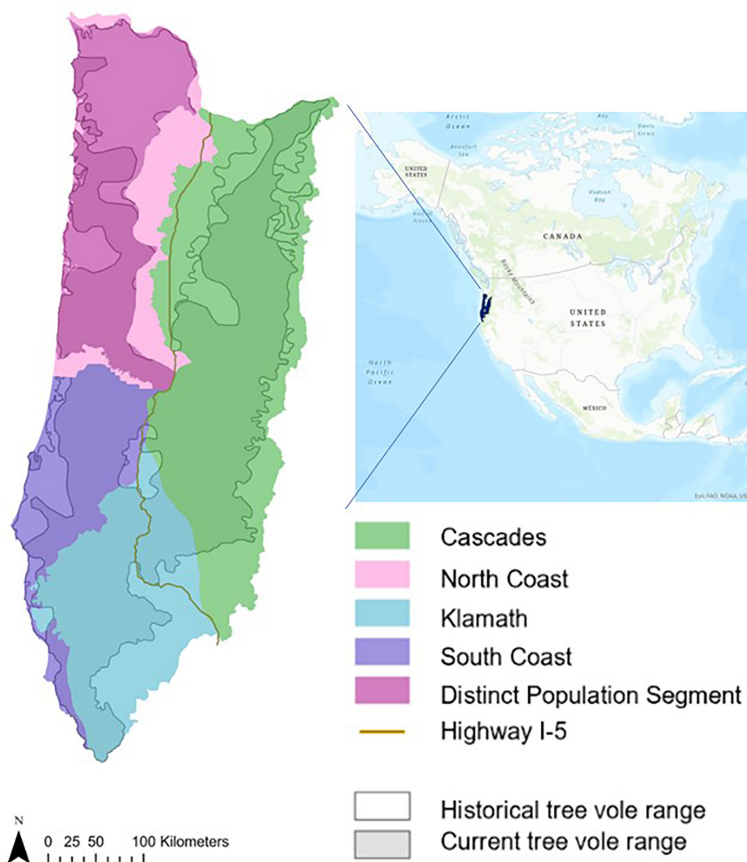


FIGURE 1 Red tree vole species distribution in the Pacific Northwest of the United States (Oregon and California), displaying the distinct population segment (DPS) and the regions by which results were summarized.

sue based on the 2019 decision and agreed to reinstate the 12-month finding to determine if the DPS warrants listing (Center for Biological Diversity, 2022). Federal agencies within the range of the tree vole have laws (e.g., National Forest Management Act) and policies (e.g., Northwest Forest Plan) with mandates or goals of sustaining biodiversity. As such, habitat considerations for tree voles have influenced forest management plans.

2.1 | Overview

To examine the degree to which habitat changes may have influenced tree vole distribution and population trends, we simulated population responses to observed habitat changes from 1986 to 2020. We developed an empirically based simulation model of tree vole demographics and life history that includes explicit interactions among individuals and their environment. Spatial and temporal variations in habitat produced dynamic resource conditions that influenced tree vole densities, density-dependent movement, survival, and reproductive success. Population abundance and habitat occupancy were emergent functions of these interacting factors. Stochastic variation in movement and demography were included as draws from probability distributions based on empirical statistical distributions. Using this spatially explicit individual-based model, we evaluated how past local and regional changes in habitat suitability influenced simulated tree vole occupancy and abundance through space and time. We conducted sensitivity analyses to assess the influence of uncertain inputs on model outputs and tested alternative model assumptions. We also iteratively removed each population region (based on physiographic provinces in the species range; Dunk & Hawley, 2009) to assess the relative contributions of populations to range-wide abundance.

2.2 | Habitat

We used a time-series of habitat suitability maps with annual variation (1986–2020) across the species' range (Linnell et al., 2023). The habitat maps were developed using a presence-only model algorithm (Maxent version 3.4) applied to annually available remote-sensing imagery, using 1096 tree vole nest locations (1995–2019), from across the range of the species. The final habitat model included forest structure and age, tree species composition, and abiotic (temperature, precipitation) covariates. Forest structure covariates that indexed presence of large old trees performed well relative to other covariates and were positively correlated with presence of tree vole nests (Linnell et al., 2023). The model algorithm was applied to

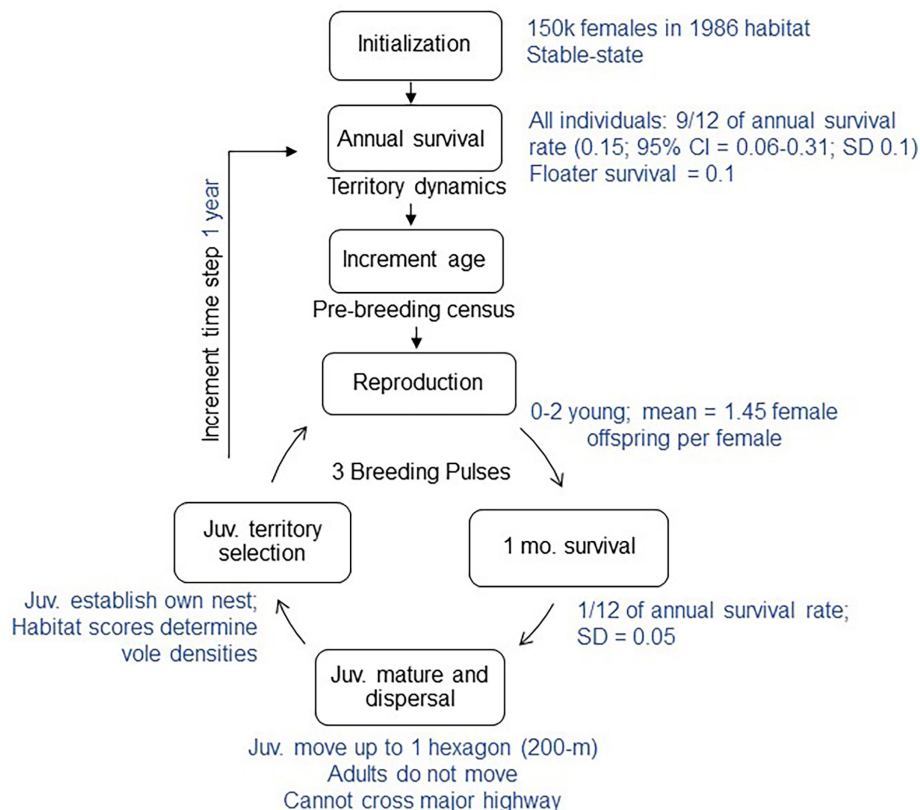
Landsat satellite imagery each year of the time-series using Google Earth Engine to produce annual habitat maps (Gorelick et al., 2017; 30-m² resolution). We tracked changes in habitat, including forest gains and losses as detected by satellite imagery, and each habitat map comprised continuous predictions of habitat suitability ranging from 0 to 100. Forest loss was typically attributable to wildfire or timber harvest, and to a lesser extent (<1%), severe windthrow, spread of forest pathogens, bark beetle infestations, or tree death from drought. The annual habitat maps represented the habitat resources with which the simulated voles interacted in the individual-based model. We resampled each annual habitat suitability map to a coarser hexagonal grid to increase computational efficiency in the spatially explicit individual-based model, constructed in the HexSim modeling platform (Schumaker & Brookes, 2018). Hexagonal pixels (hereafter, hexagons) were 200-m wide (thus, 3.46 ha/hexagon), representing a maximum potential movement distance. We used continuously distributed habitat suitability values in the individual-based models, whereby higher values represented more optimal habitat conditions. For example, we assumed tree voles would establish territories in hexagons where habitat suitability values were higher.

2.3 | Individual-based model

We conducted a literature review to identify key life history events and data by which to parameterize a two-stage (juveniles, adults), females-only model. We reviewed dozens of peer-reviewed journal articles and associated maps and datasets and selected the best available inputs (maps, statistical estimates, thresholds) that aligned with the design of our model (citations below). We programmed the model to represent an annual cycle of events (Figure 2) whereby each year, tree voles survived, aged, and reproduced in three breeding pulses. In each breeding pulse, adults reproduced, and their surviving offspring matured, dispersed, established their own territory, and reproduced in the subsequent (one or two) breeding pulses in that year. At the end of three breeding pulses, the simulation year was incremented, and the flow of events was reinitiated. The time series of habitat maps used in these events influenced individual states, movement paths, and territory selection.

Across their range, tree voles are clustered in optimal habitat (Forsman et al., 2019). Because historical occupancy and abundance records were incomplete, we could not use them to structure simulated distributions to replicate the 1986 starting conditions in the model. Instead, to

Baseline Model



annual survival rates (e.g., apparent survival rates of 0.03; Durham, 2019). Each year, individuals were assigned an annual survival rate drawn from truncated normal distributions (known fate survival mean = 0.15; 95% CI 0.06–0.31; SD = 0.1; Swingle et al., 2010). Stage-specific survival rates were not available. To represent mortality of individuals before and during the breeding pulses, we exponentiated this rate to represent the 9 months outside of the breeding season ($0.24 = 0.15^{(9/12)}$; SD = 0.05), as well as the three 1-month survival events (3 events: $0.85 = 0.15^{(1/12)}$; SD = 0.05) during breeding pulses. Survival was not scaled with hexagon suitability in baseline simulations because data demonstrating this relationship has not been evaluated.

We simulated adult females to produce three litters per year, each yielding 0–2 female offspring, approximating field data (Forsman et al., 2009). In each breeding pulse, breeders were assigned a litter size, drawn from a distribution (mean 1.45 female offspring/adult female; based on a mean 2.9 male and female young per litter; Maser et al., 1981). Juveniles that survived their first month of life matured and dispersed a short distance to secure a breeding territory (see Section 2.5). Juveniles from the first two breeding pulses became reproductively active and produced their own litters in that year's subsequent breeding pulses. This approximated the number of offspring born each year,

Most tree voles have a life span of less than a year (Swingle, 2005; Swingle & Forsman, 2009), with low

produced by overlapping successive litters (Forsman et al., 2009; Miller et al., 2010).

2.5 | Juvenile dispersal and movement barriers

Tree voles are highly dispersal-limited, generally moving 3–75 m from their original location (Swingle, 2005) and only occasionally longer (max. observed dispersal = 340 m.; Biswell, 1994), with limited movement across the ground. As such, forest fragmentation and loss generally increase movement resistance and decrease access to patches of older forest (Forsman et al., 2016; Linnell et al., 2017), for example, as a result of commercial thinning that reduces tree cover and forest stand age to <20 years. To approximate localized movement, simulated juveniles could move 0–1 hexagons (up to 200 m) from their natal nest. Individuals could not cross or build a territory using hexagons that intersected the major interstate highway (I-5) that divides the tree vole range (Figure 1).

2.6 | Territory selection and density

Dispersing individuals selected an adjacent hexagon within which to establish a territory by calculating which hexagon had the most available resources. This calculation considered the habitat score as well as the density of tree voles within that hexagon. Simulated tree voles selected the hexagon that optimized their fitness, that is, the hexagon score divided by the number of occupants. The number of tree voles that could establish a territory within a shared hexagon depended on the hexagon's suitability value. Hexagons with habitat suitability values above 40/100 indicated likely suitable habitat (Linnell et al., 2023) and were available to simulated tree voles for territory construction in the baseline model. We assumed that higher suitability indicated better resource conditions that support higher densities of tree voles. Up to five female tree voles could occupy a suitable hexagon, provided each tree vole could secure sufficient resources (score of 15). We did not simulate the creation of specific active or inactive nests, rather we tracked individuals and their use of space. Together, this set of parameters limited the possible density of tree voles to empirical bounds of 1, 3, or 5 female tree voles per hexagon in the lowest, mean, and highest suitability hexagons (respectively), corresponding to 1, 1.9, or 2.9 male and female tree voles per hectare (mean of 1.9 tree voles per ha; Marks-Fife, 2017); <1–1 per ha, (Maser, 1966), with territory sizes $1732 \pm 366 \text{ m}^2$ (Swingle, 2005; Swingle & Forsman,

2009). As density estimates were uncertain, we developed alternative scenarios that explored higher densities (see Section 2.8). If minimum resource conditions were unavailable to establish a territory within a tree vole's search radius (200-m; 1 hexagon), the individual was deemed a nonreproducing “floater” and incurred an additional survival penalty (survival rate = 0.1) after annual survival rates were applied. Floaters were retained in the model as they can make important contributions to population dynamics (Noonburg & Anderson, 2021). Occupancy and movements of simulated individuals were restricted to the current range of the species (i.e., within the last half-century; Forsman et al., 2016).

2.7 | Site fidelity and habitat change

At the end of each year, the habitat map was replaced with the next map in the time series, and the event sequence restarted with annual survival, breeding pulses and juvenile dispersal. Young of the year chose territory locations based on habitat distribution in the year they were born. If born into former or degraded habitat (only possible in the first breeding pulse), the juvenile searched for a more optimal location within their dispersal range. Once a simulated tree vole established a territory, site fidelity was maintained. We had little empirical data to parameterize detailed tree vole responses to habitat disturbances. We assumed that adults in former habitats that became reproductively inactive did not immediately die in affected locations. Future scenarios could further explore the implications of these assumptions and refine how tree voles respond to habitat change as additional information becomes available.

2.8 | Scenarios and simulations

We developed several alternatives to the baseline parameterization to evaluate the degree to which uncertainty in parameter estimates, modeled relationships, or assumptions influenced results. We evaluated scenarios with larger dispersal distances, lower floater survival, and four alternatives that modified survival rates, variability, or scaling relative to habitat suitability (Table 1). We also estimated the relative contributions of different parts of the tree vole range to species abundance by iteratively removing each region. For all simulations, we tracked female traits, states, and locations through 36 years, and conducted 100 replications for each scenario. We tallied occupancy, densities, and abundance each year and compared changes in simulated tree vole occupancy through time. We summarized these results within hexagons and within regions (Cascades, North

TABLE 1 Scenario parameterization differences among baseline and alternative scenarios for the HexSim red tree vole model.

Scenario name	Type of change	Baseline parameterization	Alternative parameterization
No floater survival	Lower survival of individuals without suitable ranges	Additional floater survival penalty; annual mortality rate = 0.9	Additional floater survival penalty; annual mortality rate = 1.0
Higher movement	Larger juvenile dispersal distance	Moved up to 1 hexagon (200 m), by exploring all adjacent neighbors	Moved up to 2 hex. (400 m) by explored 20 hex. (nearest 2 concentric hexagon rings)
Vole density independent of suitability	Increased number of voles that can occupy the same hexagon	Density scaling: linear scaling with suitability map scores above habitat threshold (40/100): Min. = 2 female limit to occupancy per hex.; Mean suitability (65) = 3 females/hex; Max. suitability (86) = 5 females/hex.	Maximum density was possible in all habitat hexagons: 5 females/hex; 3.46 ha/hex. Density was not scaled with suitability.
Survival scaled with suitability—limited stretch	Survival rates scaled with habitat suitability scores—above the habitat threshold	Max. survival rate (0.3) if occupying a hexagon score of ≥ 85 , based on annual survival estimate of mean 0.16; CI = 0.06–0.31 from (Swingle et al., 2010).	Linear interpolation: Min. survival (0.05) at 40/100; Mean survival (0.15) at 65/100; Max. survival (0.3) at 85/100
Survival scaled with suitability—full stretch	Survival rates scaled with habitat suitability—below the habitat threshold (20—max. suitability)	At the habitat threshold (40), voles received min. survival rates (0.05) that linearly increased with habitat hexagon values.	Min. survival (0.05) at 20, linear stretch of survival rates with suitability values above 20.

Coast, Klamath, South Coast, per Forsman et al., 2016). We also included the DPS as a unit of spatial summary to compare changes in this population to others in the species range.

3 | RESULTS

3.1 | Baseline population trend

The simulated tree vole population was abundant, with approximately 200,000 females distributed across the species range. Baseline parameter inputs resulted in a slight decline in abundance over the simulated timeframe (Figure 3). Individual simulation repetitions demonstrated stochastic interannual fluctuations in abundance caused by demographic stochasticity that were still evident when averaged (Figure 3; baseline scenario, 50% of data around the mean of 100 replicates). Rates of decline varied across the species range. Simulated populations in the largest region, the Cascades, lost over 40,000 female tree voles over the 36 years of landscape change (−43%). Klamath lost over 10,000 (−33%), and the South Coast (−28%) and the DPS (−25%) each lost ~5000 females relative to their 1986 populations. The DPS constitutes much of the area of the North Coast physiographic province, with few simulated tree voles

occurring outside of the DPS in this region. Declines in abundance from the starting point of a steady population state indicated incremental changes in the carrying capacity that are occurring at difference rates in different places. Rates of decline ranged from 0.7% (in DPS) to 1.2% (in Cascades) per year from a steady (1986) population state, averaged over 36 years.

3.2 | Dynamic occupancy

The simulated tree vole population was well distributed across the species range after initialization, with clustered occupancy and patchy vacancies. Not all habitat was occupied at the start or end of simulations. Some habitats had little or no occupancy (Figure 4; blue), whereas others supported a high density of tree voles (Figure 4; dark purple). Over the three past decades of disturbance and vegetation succession, the spatial patterns of occupancy changed. Habitat loss occurred throughout the tree vole range, with large impacts of timber harvest and wild-fire (Linnell et al., 2023). Blocks of interspersed public and private lands became more pronounced through time as habitat loss occurred in a checkerboard pattern, with tree voles occupying forests that were not harvested during previous decades (Figure 5). The impacts of wildfires on habitat loss also were evident in habitat and

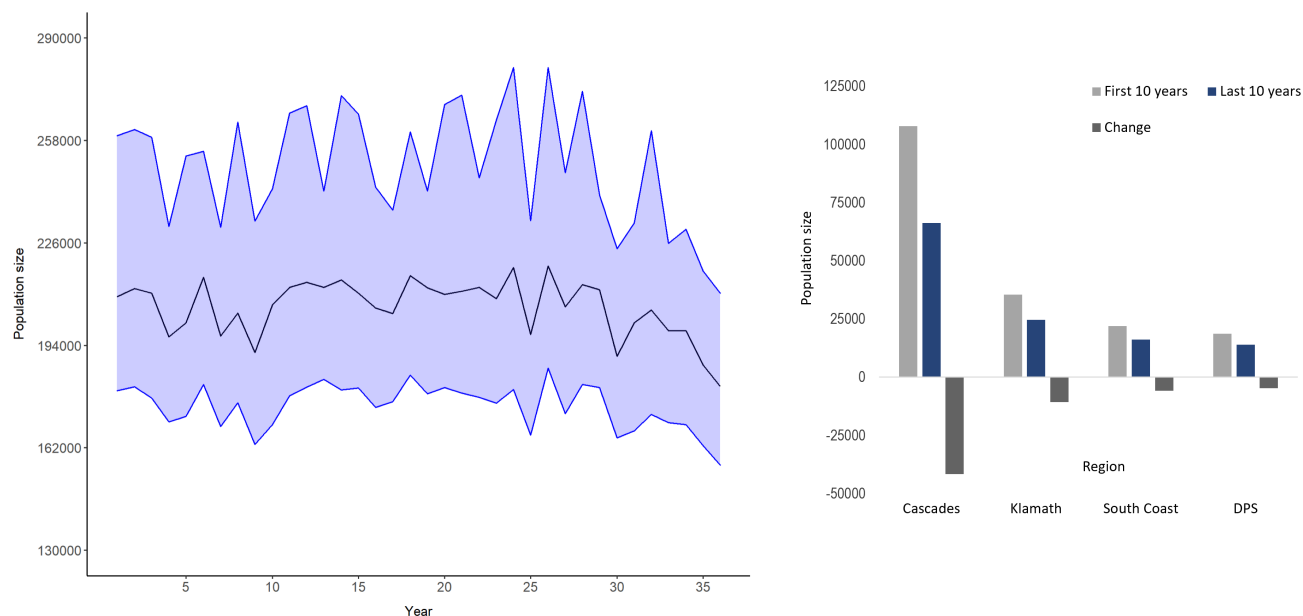


FIGURE 3 Simulated red tree vole population trajectory through 36 years of habitat change (left; baseline scenario), displaying 50% of the population size data around the mean from 100 replicate simulations; and (right) change in mean population size caused by the iterative removal of each region.

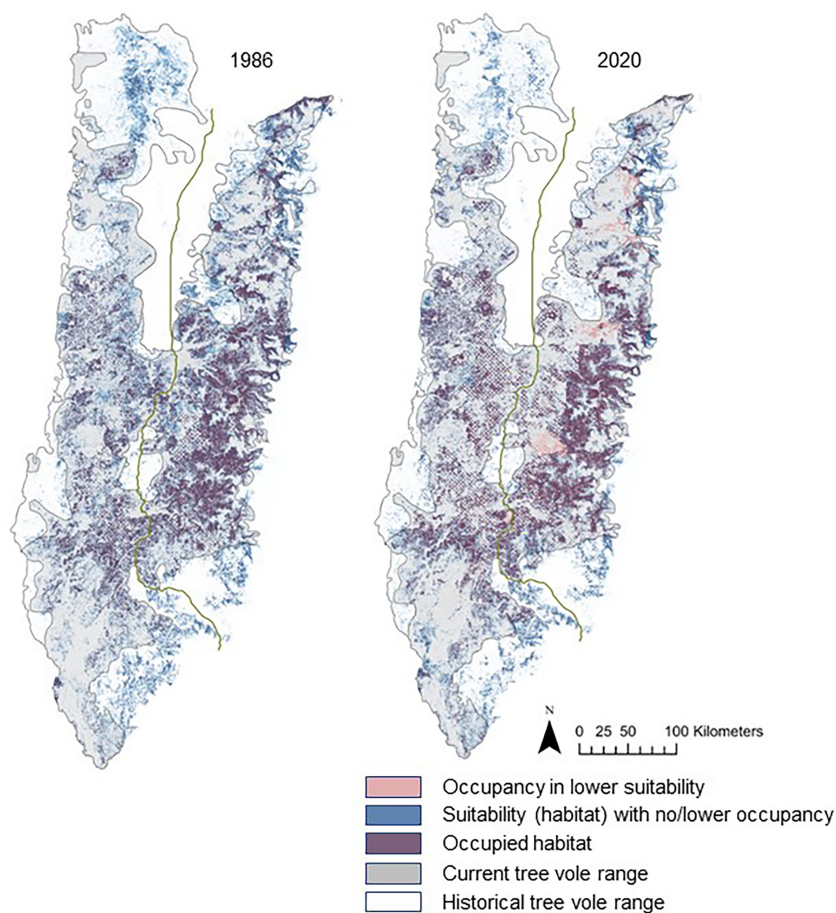


FIGURE 4 Red tree vole habitat (blue) and simulated occupancy of habitat (purple) through 36 years of landscape change in Oregon and northern California, from left) 1986 to right) 2020, with highway I-5 bisecting the species range. Color intensity indicates habitat suitability (blues), and density of tree voles (reds). Higher occupancy of higher suitability habitats appears in purple. Gray and white indicate nonhabitat. Light red areas indicate low-suitability areas with simulated tree vole occupancy.

FIGURE 5 Effect of timber harvest in block sections on simulated habitat occupancy at 1986 (left) and 2020 (right). Higher habitat suitability = darker blue; and simulated red tree vole occupancy (higher occupancy = darker red). Darker purple areas indicate the occupancy of higher suitability areas; light red indicates low occupancy in poor suitability areas. Blue indicates unoccupied or minimally occupied habitat.

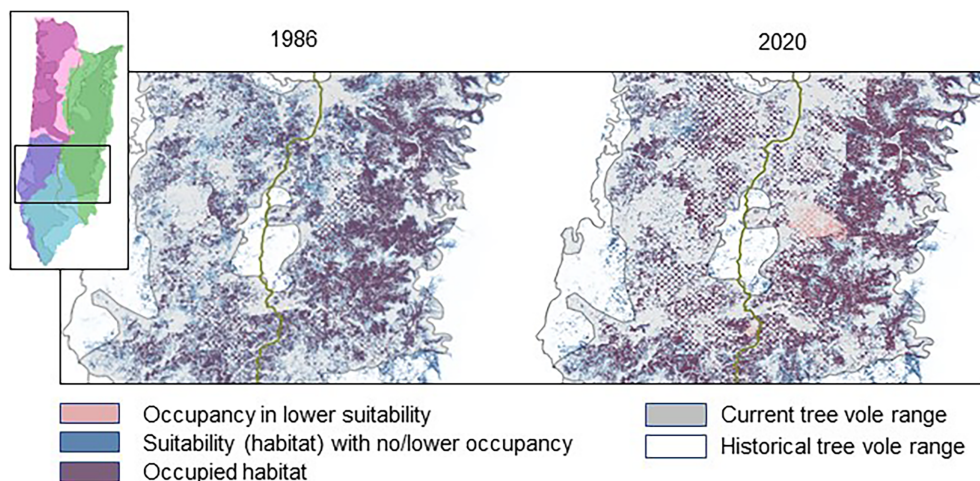
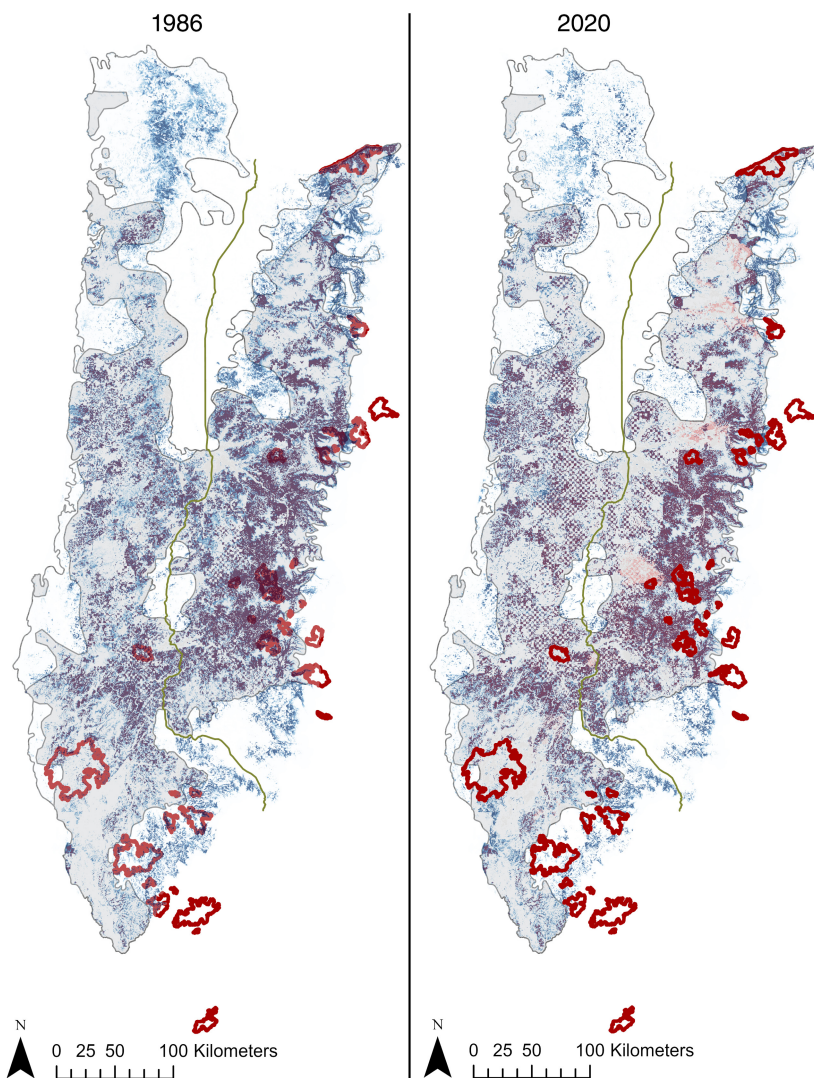


FIGURE 6 Effect of wildfire on simulated habitat occupancy at 1986 (left) and 2020 (right). Shifts in occupancy were caused by wildfire over 36 years, including fire activity in 2017 (red burn perimeters). Higher habitat suitability = darker blue; and simulated red tree vole occupancy (higher occupancy = darker red). Darker purple areas indicate the occupancy of higher suitability. Light red indicates low occupancy in poor suitability areas. Blue indicates unoccupied or minimally occupied habitat.



occupancy patterns. Over the simulation timeframe, wildfires affected tree vole habitat particularly in the Klamath, South Coast, and Cascade regions. Even decades after fire,

previously burned areas had few remaining or recovered tree vole populations at the end of simulated time series (Figure 6).

TABLE 2 Relative contributions of regions to simulated range-wide abundance of red tree voles.

Relative contribution				Area-standardized contribution	
Rank	Region removed	Area (km ²)	Reduction in abundance ^a	Mean voles lost/1 km ² area removed	Mean area removed (km ²) for loss of 1 vole
1	Cascades	32,907	100,000	3.1	0.32
2	Klamath	17,587	40,000	2.27	0.44
3	South Coast	11,383	20,000	1.78	0.57
4	Distinct Population Segment	15,734	25,000	1.59	0.63

^aRounded to the nearest 5000 to represent the approximate rather than absolute change in abundance among scenarios.

3.3 | Relative contributions to landscape capacity

Omitting individual regions in the simulations reduced overall abundance by varying amounts, indicating each region's mean contribution to range-wide carrying capacity (Table 2; Figure S1). Removal of the Cascades, the largest region, resulted in the largest overall population reduction and the highest number of tree voles lost per area removed. By contrast, the removal of the distinct population segment caused moderate population losses and resulted in the fewest tree voles lost per unit area. Differential contributions among modeling regions reflected habitat suitability, affecting maximum tree vole densities, as well as the amount of occupiable and occupied habitat within each region.

3.4 | Model sensitivity

Results were relatively robust to changes in input parameters and alternative model structures that modified key assumptions. The baseline population trend was consistent among model variations; however, simulated abundance differed among some scenarios (Figure S2). There was little difference in outcome between the baseline and a scenario that scaled survival with habitat suitability, and the no floater scenario that removed individuals that did not secure an adequate home range (i.e., floaters). The population size increased when dispersal capabilities increased from 200 m to >400 m and when simulated tree voles were able to occupy and survive in lower quality habitat (i.e., suitability scores of 20–40/100, including some young forest). Species abundance was most sensitive to tree vole density assumptions. In particular, the largest change in population size was caused by relaxing the assumption that density scales with habitat suitability. This scenario allowed the maximum observed density of tree voles to occur in any habitat, regardless of the habitat suitability value.

4 | DISCUSSION

We developed a dynamic habitat–population model to evaluate the influence of long-term landscape change on the abundance and distribution of a species that is sensitive to forest disturbance. Simulated occupancy was influenced by the spatial patterns of habitat change and accessibility of remaining habitats. Timber extraction, wildfire, and development all caused habitat loss and fragmentation through space and time (Forsman et al., 2016; Linnell et al., 2023). This was visually discernable in the simulation model as an intensifying pattern of tree vole occupancy on federal lands, that was increasingly divergent from privately owned forest lands in southwest Oregon. In this region, forest lands were primarily composed of Oregon and California Railroad Lands, with federal lands interspersed in a checkerboard pattern with private industrial forest lands (Blumm & Wigington, 2013). In the red tree vole range, most federal lands were established as late-successional reserves under the Northwest Forest Plan (Spies et al., 2019) and were far more structurally complex forests compared to adjacent industrial timber lands (Griffey et al., 2020). Federal lands supported longer-term occupancy by simulated tree voles, whereas many local extirpations were associated with non-federal lands with shorter harvest intervals. The impacts of this checkerboard pattern of forest fragmentation (Blumm & Wigington, 2013) could be particularly consequential for tree voles and other arboreal and dispersal-limited species, where dispersal among blocks relies largely on the small amount of connected habitat at checkerboard corners (Linnell & Lesmeister, 2019). In general, the increasingly patchy occurrence of tree vole populations, as seen in simulations, highlight the importance of forest management plans that prioritize imperiled species' needs for optimal patch sizes, qualities, and connectedness, while accounting for unexpected losses particularly due to large wildfires and other disturbances.

The Cascades had the largest contribution to range-wide abundance in our tests of modeling-region removal

scenarios, indicating the importance of this region to range-wide abundance at the start of simulations (1986, when removal simulations were conducted). This reflected the availability and suitability of habitat and high potential abundance of tree voles in that region relative to other regions. The Cascades likely had more high-density clusters of tree voles than other regions that served to elevate overall occupancy across the region. However, the Cascades also experienced much change from 1986 to 2020. Declines in tree vole abundance were most evident in the Cascade region and corresponded to observed habitat changes in this region (Linnell et al., 2023). For example, the 2020 Labor Day megafires were particularly devastating for old forest associated species. During a 2-week period, five fires covering approximately 340,000 ha burned mostly in high-severity patches under extreme weather conditions (Reilly et al., 2022). As a result of persistent and large-scale disturbances, the contribution of the Cascades to range-wide tree vole abundance may now be reduced, particularly if habitat changes occurred within high density population clusters. However, the remaining habitat in the Cascades likely has increasingly greater per-unit-area value to the species.

To our knowledge, this is the first comprehensive effort to assess the potential capacity of the landscape to support tree voles across the species' range. We found that the capacity of the landscape to support tree vole populations declined through the simulated study period, across land ownerships, as forest loss generally out-paced recovery after disturbance. Range-wide decreases in abundance were not large; however, larger shifts in occupancy and density patterns were discernable across the species range. Generations of simulated tree voles were able to adjust their territory locations in response to habitat change, where unoccupied habitat was accessible, resulting in dynamic clusters of occupancy. However, continued habitat loss and fragmentation could trigger a threshold response causing disproportionate population losses (Fahrig, 1997). Spatially explicit individual-based models have been used to anticipate hypothetical landscape thresholds for population extinction (Heinrichs et al., 2016; Marcot et al., 2013; Rocha et al., 2021; Vergara et al., 2015), and could be used to evaluate if and when a landscape-population threshold could cause a precipitous decline in tree vole abundance. Such future projection scenarios could include spatial habitat changes based on forest harvest and management plans, and the effects of climate change including altered fire regimes.

This model included a few key ecological assumptions that could be modified with additional data. For example, the model did not represent behavioral or fitness responses to different kinds of disturbances including

avoidance of edges, emigration, and survival impacts, as these remain mostly unstudied for this species. When such data are available, these responses could be included and may be important in assessing functional connectivity, abundance, and occupancy.

Simulated occupancy and distribution represented plausible locations of tree vole populations but were not based on known occupancy locations due to incomplete spatial-temporal coverage of these data. Empirical studies reveal many unoccupied suitable habitats, especially in the north Oregon Coast Range (Linnell et al., 2017; Linnell & Lesmeister, 2019; Price et al., 2015) and the reason for patchy occupancy appears to be legacy of historical large megafires and subsequent intensive forest management practices (Forsman et al., 2016). Our model simulated random occupancy of habitats, mimicking a patchy distribution, but did not attempt to depict known clusters of presences and absences. Hence, simulated densities could differ from the observed occupancy and density of tree voles. Where data are available, models for species with clustered occupancy of habitat may consider initializing simulations with a known abundance and distribution to project the fates of specific population clusters.

Some unknowns about tree vole ecology mattered more than others and affected our estimates of simulated range-wide abundance. Assessments of landscape capacity and abundance would benefit from an improved understanding of the density and survival of tree voles in different types or qualities of habitat, including the long-term and successful use of low suitability areas including young forests, and the ability of tree voles to survive and emigrate following disturbances such as logging, development, and fire (e.g., Durham, 2019; Willson & Forsman, 2013). Sensitivity analyses indicated that abundance could be higher if tree vole density is not related to habitat suitability, if movement distances are larger, or if tree voles are able to persist in young forest (Figure S1), although we did not find empirical evidence to suggest these relationships. Conversely, abundance could be lower if demography scales linearly with habitat selection or quality. As empirical population estimates (i.e., density, population locations) were unavailable across the range, studies that provide insight on habitat-population relationships could increase the accuracy of modeled projections of tree vole density, distribution, and abundance. We integrated available information in a coherent habitat-population model that narrowed the suite of possible realities that represent a breadth of major uncertainties. This base model can be modified as more information is accumulated on tree vole demography and abundance and used to reduce uncertainty when used as a decision-aiding tool for forest management planning.

We built a parsimonious individual-based model that linked dynamic habitat change with individual- and species-level responses to examine the impacts of disturbance on abundance and distribution. This relatively data-light parameterization reflected the integration of much of the limited data describing this species ecology but did not require parameterization of variables or mechanisms that were superfluous to how ecology was intended to be represented (i.e., it was not data-demanding). Despite its conceptual simplicity, this approach yielded ecological insights that would otherwise have been missed with approaches that omit population dynamics, movement mechanics, and constraints on habitat occupation. We found this approach to be particularly useful in translating timeseries maps of habitat changes into population estimates of abundance, occupancy, and landscape capacity. The inclusion of annual habitat maps represented small, incremental changes in habitat amount and distribution. Populations were dynamically coupled with habitat changes and resulted in emergent population sizes and distributions that reflected both subtle and large-scale landscape changes. With this construction, the IBM dynamically calculated population change metrics that would otherwise be challenging to manually estimate, particularly on an annual basis, while assessing movement constraints and accounting for resource-dependent changes in population densities. The tree vole model provided insights on how population trends differ among regions, and how habitat fragmentation can impede occupancy. Further, the simulation experiments were useful in estimating the relative contribution of each region and the distinct population segment to overall population size and stability.

5 | CONCLUSIONS

Disturbances to old-growth forests continue to reduce and constrain the distribution, abundance, and persistence of sensitive wildlife. The legacy of past changes, contemporary conditions, and projected future changes in habitat will impact sensitive forest species like the tree vole. Our results emphasize the need to anticipate future changes to design future landscapes that include wildlife. Forward-looking and malleable plans are needed to spatially design protected habitat networks that can buffer the impacts of future changes, and target areas for long-term enhancement and restoration. Our results also highlight the long-term impacts of wildfire and timber harvest on arboreal species, as well as the need to evaluate how these threats could continue to re-shape species' distribution and persistence. Experimental model systems, such as spatial IBMs, could contribute to planning efforts by providing a means to evaluate alternative forest changes

and management scenarios, and their impacts on species, as plans are developed. More specifically, the tree vole model could be used to support potential modifications of the Northwest Forest Plan (USDA and USDI, 1994) that has served to protect significant locations and portions of the tree vole's habitat on federally managed forest lands (Forsman et al., 2016) and spurred the development of strategic surveys of this and other species closely associated with older forests of the region (Olson et al., 2007). Should the Northwest Forest Plan be revisited, the tree vole IBM could serve to evaluate tree vole responses and habitat conditions needed for population persistence.

Estimates of abundance, distribution and carrying capacity are important for conservation planning but are seldom rigorously quantified for data-light species in dynamic environments. This dynamic IBM provides an example of a modeling approach that can be adapted to many other species and systems and used to develop transparent and ecologically informative assessments of the varied impacts of landscape change. This approach integrates available ecological data to explicitly link habitat and population conditions, makes ecological assumptions clear, tests alternatives to quantify their importance, and defines variation and uncertainty around the projected population outcomes. As such, it is suited to support forward-looking conservation planning to anticipate the locations and populations, pace, and magnitude of population changes.

AUTHOR CONTRIBUTIONS

Bruce G. Marcot, Damon B. Lesmeister, Julie A. Heinrichs: Conceptualization, methods, model design, interpretation, editing. Julie A. Heinrichs: Analysis, writing, visualization. Bruce G. Marcot, Damon B. Lesmeister: Project administration, funding acquisition. Mark A. Linnell: Spatial data curation, interpretation, writing, editing.

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CONFLICT OF INTEREST STATEMENT

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

DATA AVAILABILITY STATEMENT

A short video of simulated dynamic occupancy and model code can be found on Dryad: <https://doi.org/10.5061/dryad.rbnzs7hgm>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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