Forest Ecology and Management 578 (2025) 122412

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Multi-scale forest heterogeneity promotes occupancy of dusky-footed woodrats in the Sierra Nevada

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ARTICLE INFO

Keywords:
Forest management
Heterogeneity
Multi-scale occupancy modeling
Sierra Nevada
Spotted owl
Woodrat

ABSTRACT

Forested landscapes are naturally heterogeneous, with the distribution of resources influencing animal habitat selection at multiple spatial scales. However, anthropogenic activities and changing disturbance regimes have reorganized how forests are structured from fine- to landscape-scales, generally with unknown consequences for forest-associated wildlife. For instance, fire suppression and selective logging in the western US has led to more homogeneous forests with fewer small patches of early-successional vegetation. As forest management aims to improve forest resilience to extreme fire and drought by restoring historical disturbance regimes and modifying forest structure through fuel management, there is a need for studies that evaluate how animals respond to forest heterogeneity at multiple scales. Here, we estimated occupancy for the dusky-footed woodrat (*Neotoma fuscipes*), an important prey species for many forest predators including the California spotted owl (*Strix occidentalis occidentalis*), relative to forest structure and composition at site-, patch-, and landscape-scales within landscapes where forest heterogeneity was created by even-aged timber management. Woodrats were more likely to occupy sites with greater canopy cover, understory cover, and hardwoods – particularly tanoak (*Notholithocarpus densiflorus*) – and smaller patches of young forest. Woodrats were also more likely to occupy mature forests in close proximity to younger forests, suggesting that young forest patches with more favorable local conditions can produce populations that recruit into adjacent, lower-quality mature forests. Our results suggest that creating small (~2 ha) patches of high-quality woodrat habitat (i.e., young forests with dense understory and hardwoods) could provide “fishing holes” for spotted owls and other predators by supporting higher woodrat densities in surrounding mature forests managed for fuels – thus helping to meet both spotted owl conservation and forest resilience objectives. More broadly, we highlight the benefits of multi-scale studies and demonstrate that restoring landscape heterogeneity, including the creation of small early-successional forests, may benefit species conservation without compromising efforts to improve resilience in forest ecosystems globally.

1. Introduction

Forested landscapes are naturally heterogeneous (Wiens, 1995), characterized by patterns in vegetation structure, composition, and configuration that vary at multiple spatial scales (Bullock et al., 2022; Gauthier et al., 2010). Accordingly, habitat selection by forest-associated animal species represents a scale-dependent, hierarchical process (Mayor et al., 2009; Orrock et al., 2000). At a local scale, individuals select for vegetation features that provide foraging opportunities, concealment from predators, and den or nest sites (McMahon et al., 2017; Schooley, 2006), which collectively determine the quality of a habitat patch (Wiens, 1989). Patch characteristics (e.g., area, perimeter, isolation) and the juxtaposition of patch types within the surrounding landscape can shape spatial structure in populations through metapopulation and source-sink dynamics (Freckleton et al., 2005; Ritchie, 1997). Landscape and patch features may also mediate competitive and predator-prey interactions between species that perceive or use the environment at divergent spatial scales (Kuntze et al., 2023; Sollmann et al., 2016; Zulla et al., 2022). Thus, scale-dependent ecological processes can have emergent consequences

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https://doi.org/10.1016/j.foreco.2024.122412
Received 21 September 2024; Received in revised form 18 November 2024; Accepted 19 November 2024

for the distribution and abundance of forest-associated species (Andrén, 1994; Boyce et al., 2003). Understanding how species select habitat across spatial scales is essential for predicting population responses to landscape changes and designing evidence-based conservation strategies (Bowyer and Kie, 2006; Rettie and Messier, 2000; Schweiger et al., 2021). However, in practice consideration of scale is rarely intuitive (Levin, 1992), and often driven by logistics rather than theory – resulting in studies limited by a focus on *priori*-selected scales or specific habitat features (Schweiger et al., 2021).

Rapid environmental changes and anthropogenic activities are redefining the structure, function, and composition of forest landscapes worldwide (Bullock et al., 2022; Seastedt et al., 2008), with some of the most pronounced changes occurring in forests shaped by natural disturbance processes (Collins et al., 2017; Steel et al., 2022). In dry forest ecosystems, spatial heterogeneity was historically maintained by wildfires that varied in frequency, severity, and size (McLauchlan et al., 2020; North et al., 2017; Steel et al., 2015). These produced a landscape mosaic of mature, large tree-dominated forests interspersed with patches of early-successional, younger forest that supported high biodiversity (Boisramé et al., 2017). However, widespread fire suppression and the elimination of historical burning practices, coupled with selective logging of large trees, has created denser, more homogeneous forests with fewer large trees and early-successional patches on many public lands (North et al., 2017; Steel et al., 2015). As a result, ecological processes are changing, often at the expense of species that occur and evolved within these naturally complex ecosystems (Devictor et al., 2008; Henle et al., 2004). Early-successional habitats, such as young forests, are an important component of many forest ecosystems as they have distinctive characteristics and can sustain high species diversity, including numerous early-successional obligates (Allen et al., 2022; Fontaine et al., 2009). Forest management that removes or artificially restores these disturbed forest areas can therefore have significant consequences for the species and processes that rely on them (Franklin et al., 2002; Swanson et al., 2011). For predators, the elimination of these early-seral stages can reduce prey diversity and abundance (Benedek and Sîrbu, 2018; Ehrlén and Morris, 2015), which in turn can reduce fitness or increase the frequency of antagonistic competitive interactions (Davies et al., 2021; Parsons et al., 2022). Therefore, understanding scales of habitat selection is essential for understanding not only the distribution and abundance of focal taxa, but may also be important for understanding the distribution and abundance of their predators.

A number of forest management approaches seek to restore the historical processes of disturbance-prone dry forests (Bullock et al., 2022; Gaines et al., 2022; Steel et al., 2022). However, it can be challenging to recreate ecosystems that resemble historical conditions as these processes developed under a different time, climate, and environment (Watts et al., 2020). Contemporary timber management and prescribed or managed fire use may emulate a natural mosaic of vegetation types by creating patches of early-successional habitat that regenerate following planting and natural reseeding (Collins et al., 2017; Gaines et al., 2022), but evidence is mixed as to whether animals respond similarly to manufactured versus natural disturbances (Farrell et al., 2019; Zimmerling et al., 2017). Quantifying habitat selection and species interactions within forested landscapes managed for timber production that contain earlier-successional patches can provide valuable insights into how to recreate historically heterogeneous forests and meet biodiversity objectives (Arroyo-Rodríguez et al., 2020; Bullock et al., 2022). This is particularly important as managers seek to improve forest resilience to extreme fire and drought by reintroducing low-to-moderate disturbance events (Collins et al., 2017; Steel et al., 2022), highlighting the need for studies that allow us to extrapolate across scales and identify mutually beneficial strategies (Bullock et al., 2022).

The dusky-footed woodrat (hereafter, woodrat; *Neotoma fuscipes*) is an early-successional species in the Sierra Nevada, California, USA, that represents one of the largest and most energetically profitable prey for a range of forest predators (Ward Jr et al., 1998; Weathers, 1996), including the California spotted owl (*Strix occidentalis occidentalis*). Woodrat consumption is linked to emergent population benefits for mature forest-associated spotted owls (Franklin et al., 2000; Hobart et al., 2019), yet woodrats themselves are typically associated with younger forests and local forest conditions (e.g., structural complexity and dense understory cover) on timber-managed landscapes that can run counter to some fuels reduction goals (Carraway and Verts, 1991; Fraik et al., 2023). Patch and landscape characteristics also play a role in facilitating these crucial predator-prey interactions. Spotted owls capture and consume more woodrats with increasing young forest and forest heterogeneity at a home-range-scale (Hobart et al., 2019; Kuntze et al., 2023; Wilkinson et al., 2023) – which may be driven by higher woodrat abundances in young forests as well as increased capture opportunities of dispersing woodrats along the edge between mature and young forests (Sakai and Noon, 1997; Zulla et al., 2022). However, while these studies suggest that multi-scale processes may be important to woodrat populations, they typically occur at limited spatial scales or are predominantly designed around habitat features most salient to spotted owls. While this is advantageous for understanding predator foraging patterns, this perspective may make it difficult to discover nuance in the linkages between prey and forest management. Further, we lack a mechanistic understanding of the underlying processes – such as source-sink dynamics – that can mediate woodrat population dynamics from a landscape context. Therefore, studies that evaluate patterns and processes across multiple spatial scales will improve our ability to develop management approaches that increase woodrat availability to spotted owls without compromising overall forest resilience.

Here, we characterized patterns in woodrat site occupancy within a heterogeneous landscape defined by a mosaic of stand ages created by even-aged timber management. We hypothesized that woodrats respond to forest composition and structure at site-, patch-, and landscape-scales. At the site scale, we predicted that occupancy would increase when dense understory and masting hardwoods were more prevalent because of greater protective cover and resource availability. At the patch scale, we anticipated that woodrat occupancy would be highest in young forests owing to greater resource availability and lower risk of predation. At the landscape scale, we predicted that occupancy would be high when heterogeneity in forest types was high and, in mature forests, when young forests occurred in close proximity because of dispersal from these high-quality patches. While many studies on small mammal populations predominantly focus on local habitat features, environmental processes and forest management decisions often occur at patch- and landscape-scales. Therefore, understanding how habitat features that vary across scales can affect occupancy may both improve our knowledge of woodrat ecology and help inform best management practices for forest restoration and spotted owl conservation.

2. Methods

2.1. Study area

Our study took place on the western slope of the central Sierra Nevada, California, USA (Fig. 1), primarily within the Eldorado Demography Study Area (EDSA), a long-term spotted owl monitoring region that encompasses ~355 km^2 of the Eldorado National Forest. Elevation in this region ranges from 366 to 2257 m, although our work primarily took place within ~1000 to 1500 m, a range that was most likely to contain abundant woodrat populations (Innes et al., 2007). Here, differences in forest management practices over time and among landownership types have formed a landscape defined by a spatially heterogeneous mix of forest conditions described in detail elsewhere (Kuntze et al., 2023; Zulla et al., 2022; Jones et al., 2021). Briefly, within public forests, a legacy of fire suppression coupled with the selective removal of large trees since the late 19th century has created contiguous and spatially homogeneous stands of mature trees (Stephens et al.,

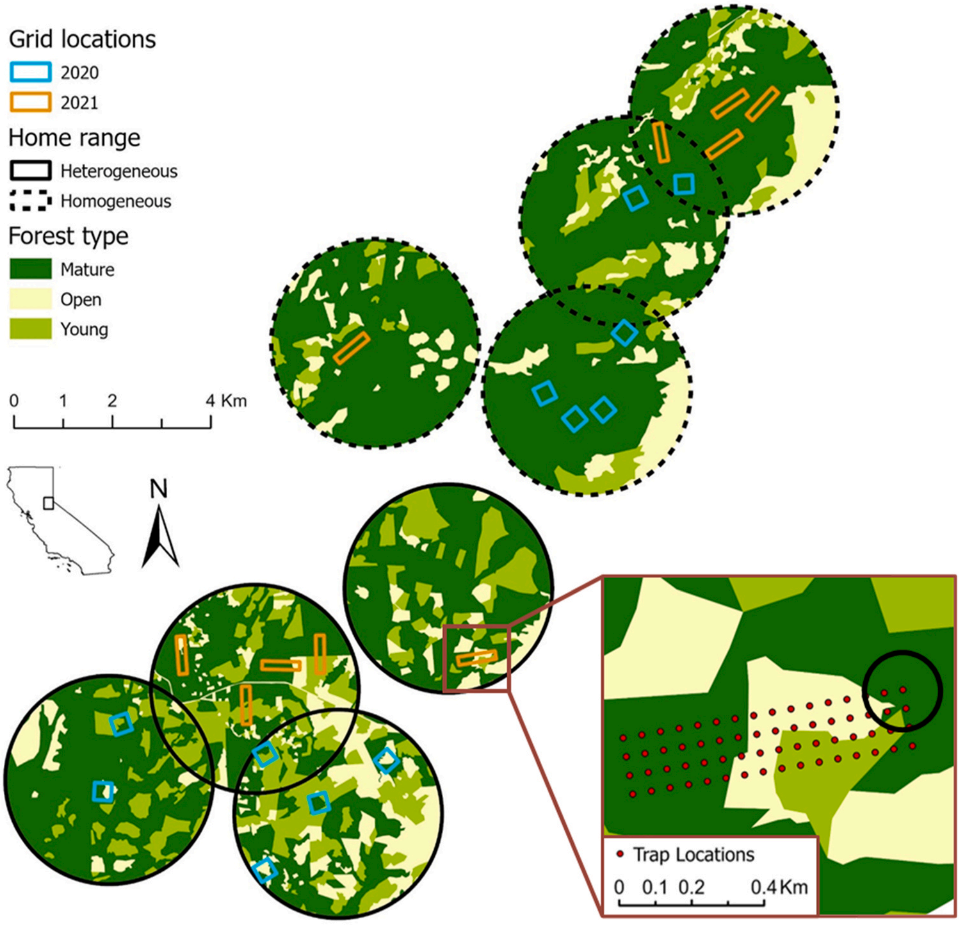

Fig. 1. Locations of trapping grids within the central Sierra Nevada, CA, USA for studying dusky-footed woodrat (*Neotoma fuscipes*) occupancy within spotted owl (*Strix occidentalis*) home ranges designated as heterogeneous or homogeneous relative to patch-scale forest types. Inset map shows the layout of a trapping grid with the black circle demonstrating the 100 m buffer within which the proportion of forest types were estimated.

2015). In comparison, on private lands frequent, even-aged timber harvesting has created a mosaic of patches that vary in size and successional stage, producing forests that are on average 30–40 years younger with less vertical structure than those on public lands (North et al., 2017).

The predominant forest type was Sierran mixed-conifer and primary vegetation included ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), white fir (*Abies concolor*), incense cedar (*Calocedrus decurrens*), Douglas-fir (*Pseudotsuga menziesii*), and several hardwood species including California black oak (*Quercus kelloggii*) and tanoak (*Notholithocarpus densiflorus*), which seldom occupy entire stands and are typically found as single trees or in small clumps among conifer associates (McDonald, 2002). This was particularly true for tanoaks, which were patchily distributed throughout the study area (Fites-Kaufman et al., 2007). Further, while black oak and tanoak each have a shrub form that allows for growth in poorer sites and at higher elevations (McDonald, 2002), in our study area the majority of tanoaks existed as dense clusters of stems emerging from a single base while black oaks predominantly existed as larger trees. Primary understory species included saplings of the aforementioned conifer and hardwood species in addition to deerbrush (*Ceanothus integerrimus*), mountain whitethorn (*Ceanothus cordulatus*), manzanita (*Arctostaphylos manzanita*), and young Pacific dogwood (*Cornus nuttallii*).

2.2. *Woodrat trapping surveys*

To characterize patterns in occupancy, we live-trapped woodrats from May through August in 2020 and 2021. We deployed grids of 64 traps spaced 50 m apart in 8×8 or 4×16 configurations (to capture a greater amount of patch edge or patch interior, respectively) within eight occupied spotted owl home ranges (Fig. 1). These home ranges were created by centering circular buffers around the most recent known nest or roost site for the respective spotted owl pair with a 2.12 km radius – equal to the median home range size of all males tagged for a minimum of 25 days (14.12 km^2) from previous studies (Atuo et al., 2019; Zulla et al., 2022). To determine grid placement within home ranges, we first used imagery from the National Agricultural Imagery Program (NAIP) to manually digitize patches of relatively uniform vegetation conditions within ArcGIS following protocols described in Tempel et al. (2014). We defined three predominant forest types based on canopy cover and size of dominant trees as follows: mature forest (>40 % canopy cover and dominant trees >12 in. diameter at breast height [DBH]), young forest (>40 % canopy cover and saplings or dominant trees <12 in. DBH), and open area (<40 % canopy cover). Then, we classified home ranges with predominantly mature forest in large, contiguous stands as 'homogeneous' ($n = 4$) and home ranges with a more even mixture of forest types and patch sizes as 'heterogeneous' ($n = 4$). These designations were supported with estimates of Shannon's diversity index, wherein forest types were more uniformly represented within heterogeneous home ranges ($\hat{H} = 0.92$, range = 0.79–1.05; mean areas = 58.8 % mature, 27.9 % young, and 12.2 % open) compared to homogeneous ones ($\hat{H} = 0.65$, range = 0.57–0.71; mean areas = 78.6 % mature, 9.9 % young, and 11.5 % open; Kuntze et al., 2023). Within homogeneous home ranges, we randomly placed grids in large contiguous stands of mature forests; within heterogeneous home ranges, we used ArcGIS and stratified trapping grids by forest type. Specifically, we centered our trapping grids along edges of (1) young and mature forest or (2) open and mature forest to ensure adequate representation of core and edge for each forest type. As part of this process, we constrained grid locations in heterogeneous home ranges to contain at least 30 % of mature forest and 30 % of either young forest or open area.

We deployed traps for six consecutive days using a paired approach in which two grids were sampled concurrently – one each within a heterogeneous and homogeneous home range. We captured woodrats in steel mesh traps (model #105; Tomahawk Live Trap Company, Hazelhurst, Wisconsin, USA) baited with a mixture of birdseed, dried fruit, and peanuts. At the initial capture, we ear-tagged and recorded age, sex, mass (g), and hind foot length for all individuals. All captures were conducted with approval from the Institutional Animal Care and Use Committee of the University of Wisconsin, Madison (IACUC #A006173-A01), and followed guidelines from the American Society of Mammalogists (Sikes et al., 2016).

2.3. Sampling environmental features and defining covariates

We conducted vegetation sampling at every trap location with a woodrat detection as well as an additional 480 locations without woodrat captures. For non-capture sites, we selected every other or every third trap location in a grid for vegetation sampling. We measured slope and aspect and confirmed the forest type assigned from NAIP imagery. We then centered circular plots with a radius of 12.5 m around sampled trap locations, within which we recorded canopy cover with a densitometer, and understory cover using a visual estimation of the proportion of ground obscured by vegetation <2 m height. For each tree within a plot, we recorded species, DBH, and condition (live, dead). We measured downed woody debris by counting the number of logs and snags within our plot >1 m in length with >10 cm DBH. We then walked a 12.5 m line-transect from the center and counted every stick that crossed the line; this provided us with a representative sample of midden-construction materials in the area. Finally, we determined whether there was a source of water within 25 m of the trap location.

At each individual site where vegetative surveys were collected, we considered covariates defined at three spatial scales: landscape, patch, and site (Table 1). Landscape covariates were estimated based on patterns in forest type (i.e., mature, young, open). For these, we first assigned a categorical variable for whether a trap was located within a 'heterogeneous' or 'homogeneous' spotted owl home range as defined by our sampling design. Next, we derived estimates of forest composition from circles of 100 m centered around each individual site (Fig. 1). This buffer size represented areas equal to the average reported area of woodrat home ranges (Innes et al., 2009; Sakai and Noon, 1997). We estimated the percentage of mature forest (Mature100), young forest (Young100), and open area (Open100) within each buffered area. Proportions were highly correlated, so while all were considered in the initial stages of model construction, we only carried forward the covariate for Young100 in our final model set. Further, to explore our prediction that source-sink dynamics from young forest would drive increased occupancy rates in adjacent mature forest specifically, we tested an interaction of this variable with forest type and report the effect of Young100 for sites within mature forest only. Patch-scale covariates included forest type and patch area (Fig. 1). Similar to the approach for Young100, we tested an interaction of patch area with forest type and only report parameter estimates for those traps within young forests. Site-scale covariates were collected during vegetative surveys and estimated within a circular plot with a radius of 12.5 m centered around each trap location. These were outlined in the 'field methods' section and predominantly represented local metrics of forest characteristics (e.g., canopy cover, basal area), protective cover (understory, downed woody debris), and resource availability (hardwoods, tanoaks, sticks).

Table 1
Covariates included in models to explore occupancy patterns for dusky-footed woodrats (*Neotoma fuscipes*) in the Sierra Nevada, California, USA.

Category	Variable	Ecological description
Landscape	Forest heterogeneity	Categorical designation (homogeneous, heterogeneous) for landscape composition of patch-scale forest types targeted by sampling design.
	Mature100	Proportion of 100 m circular buffer comprised of mature forest
	Young100	Proportion of 100 m circular buffer comprised of young forest – for mature forest
	Open100	Proportion of 100 m circular buffer comprised of open area
Patch	Forest type	Forest type defined by NAIP imagery classification (mature, young, open)
	Patch area	Total area of the forest type patch (km^2) – for young forest
Site	Canopy cover	Proportion of sky (%) obscured by vegetation >2 m height within 12.5 m
	Understory cover	Proportion of ground (%) obscured by vegetation <2 m height within 12.5 m
	Basal area	Total basal area (m^2; measured with DBH) of all live and dead standing trees <2 m tall within 12.5 m
	Hardwoods	Total live basal area of hardwoods within 12.5 m
	Masting hardwoods	Total live basal area of hardwoods >28 cm DBH within 12.5 m
	Tanoaks	Total live basal area of tanoaks within 12.5 m
	Sticks	The number of sticks along a 12.5 m line-transect from the center
	Downed woody debris	Number of logs and snags >1 m length and >10 cm DBH within 12.5 m
Physiography	Slope	Average of upslope and downslope measurements (°) from plot center along aspect
	Elevation	Elevation (m) at plot center
	Water	Presence of water within 25 m as factor (yes, no)
Other	Julian date	Julian date of sampling night
	Lunar cycle	Phase of the lunar cycle during sampling night, measured by the number of days since a new moon (0; new moon – 15; full moon)
	Sampling season	Sampling year (2020, 2021)
	Secondary sampling period	Sequential trapping night of a grid deployment (T; 1, first night – 6, final night)
	Home range ID	Individual ID for home range (corresponding to each unique owl pair)
	Grid ID	Individual ID for trapping grid

2.4. Multi-stage occupancy modeling framework

We employed a stepwise, multi-stage approach to model woodrat occupancy as a function of environmental conditions at the three spatial scales while incorporating detection probabilities to account for imperfect detection (MacKenzie et al., 2017; Morin et al., 2020; Pavlacky Jr. et al., 2012). We used the unmarked package (Fiske and Chandler, 2011; Kellner et al., 2023) in program R (R Core Team, 2023) to fit single-species, single-season occupancy models and estimate the probabilities of detection (p) and occupancy (ψ). We treated each trap-night as a sampling period, and recorded whether a woodrat was detected (1) or not detected (0), or if a trap was not functional from disturbance or bycatch (NA), in which case we censored that night's observation. Occupancy models assume population closure where there is no immigration, emigration, or mortality at the time of the study (Royle and Dorazio, 2008). Given the small home ranges, limited dispersal, and low mortality rates of this population (Kuntze et al., 2023; Sakai and Noon, 1997), as well as the short duration (6 days) of each trapping survey, we considered this assumption likely satisfied. At each stage, we constructed model sets for all combinations of relevant variables, then progressed covariates from the best model structure forward to be tested within the final stage. All continuous variables were standardized. To address multicollinearity, we excluded highly correlated covariates (|r| >0.6) from the same model (Dormann et al., 2013). We ranked models using Akaike Information Criterion (AIC; Burnham and Anderson, 2002), and considered any model that outperformed the null and was within 2 ΔAIC of the top model to be competitive (Morin et al., 2020). Our staged approach was as follows:

Stage 1. Determine model structure for detection. In this stage, we held ψ constant while *p* was allowed to vary based on covariates. We included a set of spatially independent covariates (sampling year, secondary sampling period, Julian date, and lunar illumination; Table 1) in these models in addition to the patch-scale forest type covariate for each trap-location. We chose to include this latter variable because woodrats exhibit behavioral differences (i.e., foraging and apprehension) between young and mature forests (Kuntze et al., 2024), which may also affect detection probabilities. In all subsequent stages, we fixed the best-supported model for detection while ψ was allowed to vary based on covariates.

Stage 2. Test physiographic covariates. Prior to inclusion of scale-specific variables within our model sets, we tested the potential influence of physiographic, scale-independent covariates for elevation, slope, and water (Table 1) on ψ.

Stage 3. Test scale-specific covariates. We modeled the effects of covariates quantified at three distinct spatial scales on ψ by constructing separate model sets for landscape- (Stage 3.1), patch- (Stage 3.2), and site-scale (Stage 3.3) variables.

Stage 4. Combine sub-stages and interactions. We carried forward all covariates included in the top models from Stage 2 and each sub-stage in Stage 3 to construct a final model suite. In this stage, we also included a number of *a priori* interactions (Table S1) between covariates within and across scales, even if one or both covariates were not supported within model sets from Stage 3. We determined the best overall model(s) for ψ and reported the associated coefficients with significance based on 85 % confidence intervals as recommended by Arnold (2010).

3. Results

Over two field seasons we surveyed 22 grids of 64 traps each for a total of 8448 trap-nights. In total, we recorded 460 detections of 236 individual woodrats. Woodrats were captured at 176 of 1408 traps. In

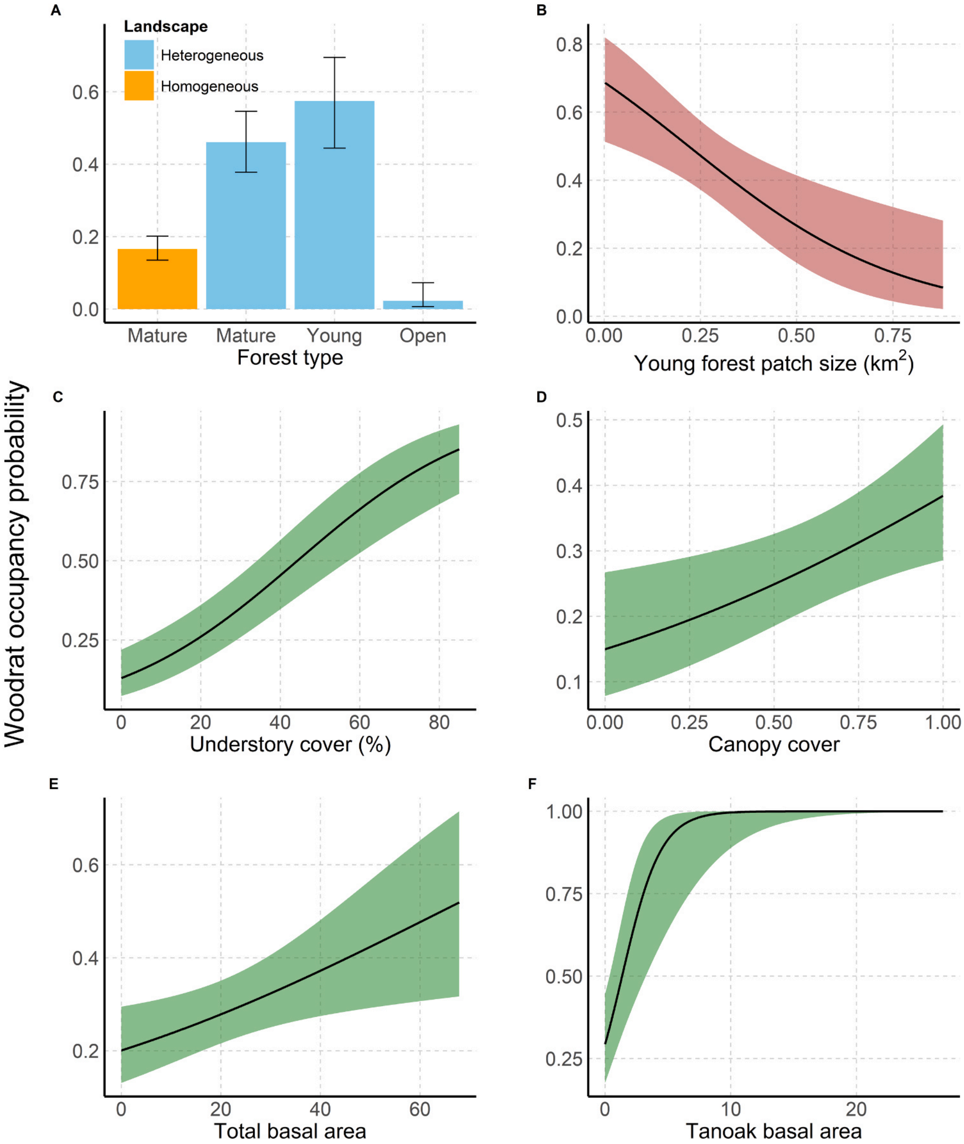

Fig. 2. Fitted values (±85 % CI) representing estimates of occupancy probability for dusky-footed woodrats (*Neotoma fuscipes*) within the central Sierra Nevada, California, USA relative to (A) forest heterogeneity and forest type, (B) patch area in young forest, site-scale (C) understory cover, (D) canopy cover, (E) basal area of all trees, and (F) basal area of tanoaks. Values were derived from the top-ranked model with additional variables held constant at mean observed values.

2020, we collected 4608 trap-nights of data (768 traps). Among those, we recorded 165 woodrat detections of 88 individuals (among 72 traps) and censored 334 trap-nights (among 237 traps). In 2021, we collected 3840 trap-nights of data (640 traps). Among those, we recorded 294 occurrences of 148 individuals (among 105 traps) and censored 647 trap-nights (among 311 traps) Fig. 2.

3.1. Multi-stage modeling

Stage 1. Determine model structure for detection: The top model for detection probability included the effect of habitat and secondary sampling period ($w_i = 0.43$; Table S2). Woodrat detection probability was greatest in young forests ($p = 0.58$ [0.53, 0.63]), followed by mature forests ($p = 0.43$ [0.30, 0.47]) and open areas ($p = 0.03$ [0.01, 0.08]). These two predictors were included in all occupancy models in subsequent stages. Competitive models (within 2 AIC) also included the effect of lunar illumination and Julian date, although these parameters were uninformative (Table S2).

Stage 2. Test physiographic covariates: The top model from Stage 2 indicated that among physiographic covariates, occupancy probability decreased with increasing elevation with no other models within 2 AIC ($w_i = 0.53$; Table 2; Table S3).

Stage 3. Test scale-specific covariates: At the landscape-scale (Stage 3.1), occupancy probability was greater in heterogeneous home ranges and increased with the proportion of young forest within a 100 m buffer with no other models within 2 AIC ($w_i = 0.75$; Table 2; Table S3). At the patch-scale (Stage 3.2), occupancy probability was greatest within young forests, followed by mature forest and open areas. Occupancy also decreased with increasing young forest patch area with no other models within 2 AIC ($w_i = 0.74$; Table 2; Table S5). At the site-scale, occupancy probability increased with understory, tanoaks, canopy cover, and total basal area of all trees ($w_i = 0.54$; Table 2; Table S5), while a competitive model excluded the effect of basal area ($w_i = 0.34$; Table 2; Table S5).

Table 2

Results from stages 2 and 3 for modeling dusky-footed woodrat (*Neotoma fuscipes*) occupancy in the central Sierra Nevada, California, USA. Models denoted by "." indicate the intercept-only (i.e., null) model. Covariates from the top model structure at each stage and substage were carried forward to all subsequent stages. Detection probability structure was held constant for all models at *p* (T, forest type).

Ψ	AIC	ΔAIC	K
Stage 2: Physiography			
Elevation	1860.75	0	6
Elevation + Slope	1861.3	0.56	7
Slope	1865.12	4.37	6
.	1869.96	9.21	5
Stage 3.1: Landscape			
Forest heterogeneity + Young100 (Mature)	1828.85	0	9
Forest heterogeneity	1831.15	2.3	6
Young100 (Mature)	1845.75	16.9	8
.	1869.96	41.1	5
Stage 3.2: Patch			
Forest type + Patch area (Young)	1839.12	0	9
Patch area (Young)	1841.21	2.09	8
Forest type	1855.2	16.08	7
.	1869.96	30.84	5
Stage 3.3: Local			
Understory + Basal + Canopy cover + Tanoaks	1748.27	0	9
Understory + Canopy cover + Tanoaks	1749.11	0.84	8
Understory + Basal + Tanoaks	1751.68	3.4	8
Understory + Tanoaks	1757.56	9.29	7
Basal + Tanoaks	1793.19	44.92	7
Tanoaks	1795.57	47.3	6
Understory + Basal	1795.95	47.67	7
Understory	1805.49	57.22	6
Hardwoods	1862.6	114.33	6
Basal	1865.31	117.04	6
Canopy cover	1868.16	119.88	6
.	1869.96	121.68	5
Sticks	1870.04	121.77	6
Downed woody debris	1870.72	122.45	6

Stage 4. Combine sub-stages and interactions: The top overall model ($w_i = 0.27$; Table 3) indicated that woodrat occupancy was lower within homogeneous home ranges ($\beta_{\text{homogeneous}} = -0.43$ [-0.80, −0.07]) and greater within young forest compared to open areas ($\beta_{\text{young-open}} = 3.59$ [2.13, 5.04]; Fig. 3A) and mature forests in homogeneous ($\beta_{\text{young-mathom}} = 1.99$ [1.20, 2.79]]) – and to a lesser extent – mature forests in heterogeneous home ranges ($\beta_{\text{young-mathet}} = 1.56$ [0.77, 2.35]). Occupancy probability was also greater in mature forests specifically within heterogeneous versus homogeneous home ranges ($\beta_{\text{mathet-mathom}} = 0.43$ [0.07, 0.80]). Within young forests, occupancy decreased with increasing young patch area ($\beta_{\text{patch\_area}} = -0.50$ [-0.82, −0.19]; Fig. 2B). Occupancy probability at the site-scale increased with increasing understory ($\beta_{\text{understory}} = 0.73$ [0.56, 0.91]; Fig. 2C), canopy cover ($\beta_{\text{canopy\_cover}} = 0.26$ [0.05, 0.47]; Fig. 2D), basal area of all trees ($\beta_{\text{basal}} = 0.25$ [0.07, 0.43]; Fig. 2E), and basal area of tanoaks ($\beta_{\text{tanoak}} = 1.24$ [0.57, 1.92]; Fig. 2F). Competitive models (within 2 AIC; Table 3) excluded the effect of either landscape-scale forest heterogeneity ($w_i = 0.17$) or canopy cover ($w_i = 0.16$); the values of the remaining parameters did not change notably in either. Additionally, other competitive models included the covariate for Young100 within mature forest, both with ($w_i = 0.13$) and without ($w_i = 0.12$) the effect of forest heterogeneity, although this parameter was not informative in either model.

4. Discussion

Large-scale forest management has the potential to affect animal habitat use in substantial ways. We demonstrated that, within forest landscapes where spatial heterogeneity is created and maintained from even-aged timber management, woodrats selected for forest structure and composition characteristics at multiple spatial scales. In particular, woodrat occupancy increased in association with elements of vegetation that provide food resources and protective cover, as well as within smaller patches of younger forests and with increasing heterogeneity. While studies on small mammals have predominantly focused on local habitat features, environmental processes and forest management decisions often occur at broader spatial scales. By systematically evaluating multiple scales of observation within a hierarchical framework, our study provides a unique perspective on habitat selection and the mechanisms that influence the population dynamics of this key prey species within a local, patch, and landscape context.

Table 3

Modeling results from stage 4 (combining substages and interactions) for dusky-footed woodrat (*Neotoma fuscipes*) occupancy in the central Sierra Nevada, California, USA. Covariates from the top model structure at each stage and substage were carried forward to this stage. The model denoted by "." indicates the intercept-only (i.e., null) model. Only competitive models (within 2 ΔAIC of the top model) are shown; variables from top models in earlier stages (i.e., Table 2) and interactions (i.e., Table S1) not shown here were still tested; noncompetitive models and covariates not present in any competitive models are not included on this table for easier interpretability. Detection probability structure was held constant for all models at *p* (T, Forest type).

Ψ	AIC	ΔAIC	K
Forest heterogeneity + Forest type + Patch area + Canopy cover + Understory + Tanoaks + Basal area	1737.22	0	13
Forest type + Patch area + Canopy cover + Understory + Tanoaks + Basal area	1738.10	0.88	12
Forest heterogeneity + Forest type + Patch area + Understory + Tanoaks + Basal area	1738.32	1.10	12
Forest heterogeneity + Forest type + Patch area + Young100 + Canopy cover + Understory + Tanoaks + Basal area	1738.67	1.45	14
Forest type + Patch area + Young100 + Canopy cover + Understory + Tanoaks + Basal area	1738.79	1.57	13
	1869.96	132.74	5

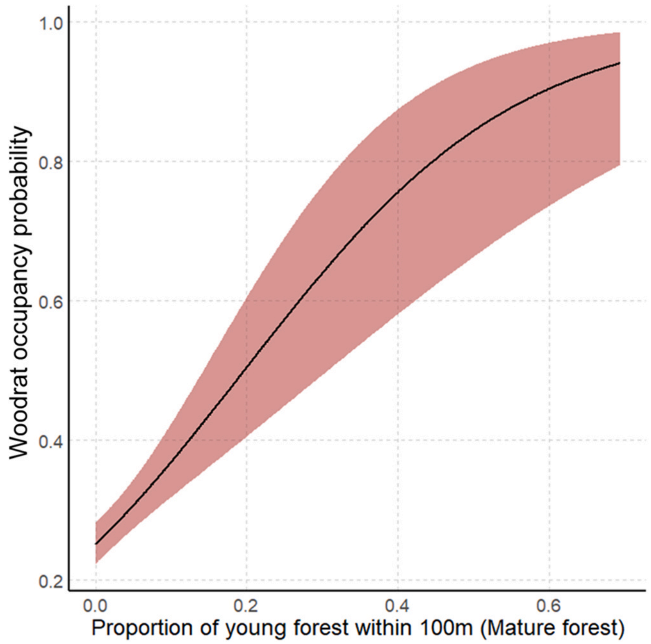

Fig. 3. Fitted values (±85 % CI) representing estimates of occupancy probability for dusky-footed woodrats (*Neotoma fuscipes*) in mature forest relative to the proportion of young forest within 100 m. Values were derived from the top model in Stage 3.2 with additional variables held constant at mean observed values.

4.1. Local characteristics

Woodrat occupancy increased in areas with dense understory and prevalent masting hardwoods, likely due to greater protective cover and resource availability (Carraway and Verts, 1991; Fraik et al., 2023), consistent with previous findings (Fraik et al., 2023; Hamm and Diller, 2009). The association with canopy cover has also been previously documented (Fraik et al., 2023; Hamm and Diller, 2009), although it is generally believed that this forest element does not have much stand-alone value to small mammals, and rather represents a proxy for areas with greater mast production or structural complexity (Sollmann et al., 2015).

In contrast to previous studies that detected strong associations between woodrats and mast-producing black oaks (e.g., Fraik et al., 2023; Innes et al., 2007; Sakai and Noon, 1993), we found that tanoak prevalence was a key component of woodrat habitat in our study area as it far exceeded the explanatory power of all hardwoods combined (Table 2). Tanoaks have characteristics that may be particularly beneficial to woodrats – especially for the variety found within the Sierra Nevada. While tanoaks along the Pacific coast (*N. densiflorus* var. *densiflorus*) can reach 20–25 m, dwarf tanoaks (*N. densiflorus* var. *echinoides*) occur at higher elevations – such as our study area – and frequently grow as a shrub less than 3 m tall (Griffin and Critchfield, 1976; Hickman, 1993). This variety of tanoak develops a multi-stem growth that produces a dense, structurally complex layer (Hickman, 1993; McDonald, 2002) that may provide dual benefits of protective cover and a foundation for midden construction at the base between stems. Under shady conditions young tanoak plants develop a more shrublike growth (McDonald, 2002; Tappeiner and Roy, 1990), suggesting that in shadier – and riskier – mature forests, the structure of tanoak provides even more protective cover when the threat of vertical predation is highest (Embar et al., 2011, Kuntze et al., 2024). Tanoaks may also produce a more favorable food crop for woodrats. Despite the name, tanoaks are not a true oak species; while their acorn mast can vary annually, their flower and seed production is prodigious and no western ‘oak’ species produces acorns as consistently as tanoaks (McDonald, 2002; Tappeiner and Roy, 1990). Acorn production can start as early as 5 years (Tappeiner and Roy, 1990), and open-grown tanoaks produce larger crops than those in shade (McDonald, 2002), which may help woodrats colonize and occupy an area quicker following a disturbance – especially when large, masting black oaks are absent. However, despite their myriad benefits, our ability to extrapolate these findings across the distributional range of woodrats may be limited as tanoaks require relatively high moisture levels and mild temperatures (Hickman, 1993), and have a relatively scattered distribution outside of lower, coastal areas (Griffin and Critchfield, 1976; Hickman, 1993). As such, woodrats and tanoak only overlap occasionally, and outside of these areas the relative importance of other hardwoods (including black oak) and processes at other spatial scales may be greater.

4.2. Patch characteristics

Woodrat occupancy was greatest in young forest patches, reflecting previously reported patterns in density and abundance (Carraway and Verts, 1991; Kuntze et al., 2023; Sakai and Noon, 1993). The benefits of younger forest to woodrats are likely the result of favorable local conditions, as younger forests contain a greater density and diversity of high-quality food resources (Carraway and Verts, 1991; Fontaine et al., 2009), stable microclimates (Swanson et al., 2011), nest-building structures and materials (Innes et al., 2007), and protective cover (Kuntze et al., 2024; Sakai and Noon, 1997). While this is true to an extent, justifying patterns in patch-scale processes as a product of local conditions alone can fail to consider the effect of patch characteristics.

Counter to theoretical expectations, woodrat occupancy decreased within larger patches of young forests. Increasing patch area is commonly associated with beneficial intrinsic and extrinsic attributes that increase occupancy, such as resource availability, territory size, and habitat quality (Garda et al., 2013; Kitchener et al., 1980). However, studies on small mammals have also detailed neutral or positive responses to decreasing patch sizes (Foster and Gaines, 1991; Nupp and Swihart, 1996), attributed to competitive release from other species or denser populations in smaller patches (Dooley and Bowers, 1996; Foster and Gaines, 1991). Woodrats were the largest-bodied small mammal in our study area, and across their distributional range are competitively dominant (Grant, 1972), even over other *Neotoma* species (Cameron, 1971). While interspecific interactions have minimal effects on population dynamics, woodrats are semi-territorial and can aggressively defend core areas against same-sex conspecifics (Innes et al., 2009; Lynch et al., 1994).Home range sizes also vary considerably among individuals (Innes et al., 2009; Sakai and Noon, 1997), and in some cases can overlap with neighboring pairs (Innes et al., 2007; Lynch et al., 1994). Home range size is often inversely related to population density among mammals (Sanderson, 1966); therefore, the increased occupancy probabilities observed in smaller patches may be a result of smaller, overlapping territories and greater woodrat densities.

In addition to occupancy probabilities, woodrat detection probability also varied with forest type and was 1.5x greater in young versus mature forests. Among predated species, forest structure can influence the perception of risk (Gaynor et al., 2019). In turn, spatial variation in predator activity can affect space use (Dellinger et al., 2019), foraging (Kotler and Blaustein, 1995), and population dynamics of prey (Ehlman et al., 2019; Garvey et al., 2020). Owls predominantly forage within mature forests (Atuo et al., 2019; Zulla et al., 2022), and woodrats occupying these areas exhibit behavioral differences (e.g., increased vigilance and decreased foraging time) compared to those in younger forests, independent of local-scale conditions including understory cover (Kuntze et al., 2024). Higher woodrat detection in young forests supports the hypothesis that habitat selection by woodrats at patch-scales is driven, in part, by the avoidance of riskier areas in mature forests (Lima and Dill, 1990; Turkia et al., 2018).

4.3. Landscape characteristics

At a broader scale we found that spatial heterogeneity – driven primarily by the juxtaposition of mature and younger forests – produced patterns in woodrat occupancy observed or hypothesized in prior work on woodrat abundance within managed forest landscapes (Kuntze et al., 2023; Sakai and Noon, 1993). In heterogeneous systems, landscape-scale abundance is an emergent property of the composition of different habitat patches, with landscapes containing a greater area of high-quality habitat patches expected to have greater abundance (Holt, 1985; Iles et al., 2018). These drivers of increased abundance likely translated to occurrence rates, as we found that the probability of woodrat occupancy was >2.5x greater within spotted owl home ranges characterized by a heterogeneous composition of forest types, consistent with findings from Kuntze et al. (2023) that documented 2.5x greater total abundance in similar landscapes. Dispersal from high-density source patches can also increase occupancy or relative densities within lower-quality patches (Holt, 1985), and in some cases, landscape-scale abundance may even exceed the combined carrying capacity of all representative patches (Zhang et al., 2017). While previous studies have proposed a similar process driven by woodrat dispersal from high-quality young forest into the surrounding landscape (Innes et al., 2009; Kuntze et al., 2023; Sakai and Noon, 1997), empirical evidence for this mechanism has been limited by a lack of adequate sample sizes or perspectives from the appropriate spatial scales. We found that woodrat occupancy in mature forest patches was 2.8x higher in heterogeneous versus homogeneous spotted owl home ranges – slightly above but still in line with the 2.3x increase in density reported by Kuntze et al. (2023). At a finer spatial scale, occupancy increased in mature forests with an increasing proportion of young forest within 100 m (Fig. 3), with the greatest effect in model sets where patch- and landscape-scale conditions were exclusively considered. Thus, our findings suggest that high-quality young forest can produce dense woodrat populations that recruit into adjacent, lower-quality mature forests, decoupling local occupancy from habitat quality.

4.4. Management implications

Our study provides insight into two management activities occurring at different spatial scales that can benefit species conservation potentially without compromising resilience in forest ecosystems. On privately owned lands managed for timber production, rotational, even-aged silvicultural practices that create landscape-scale heterogeneity – as a mosaic of mature forests, young forests, and open areas that develop into younger forests – may foster higher woodrat occupancy within mixed-ownership landscapes like our study area. This, in turn, could increase woodrat abundance and availability to spotted owls with emergent benefits to fitness, occupancy, and space use (Conner et al., 2016; Hobart et al., 2019). This conclusion is supported by other studies that have demonstrated the benefits of promoting landscape heterogeneity on the scale of a spotted owl home range, especially in areas where woodrats represent a dominant prey species by biomass (Hobart et al., 2019; Kuntze et al., 2023; Zulla et al., 2023).

In addition, on public lands such as national forests where rotational, even-aged timber harvesting is not a management tool, managers could employ silvicultural techniques such as group selection harvests to create small openings (~2 ha) on the landscape while managing the surrounding forests for fuels reduction goals. This patch size recommendation is supported by direct observations of commensurate young forest patches that contained ≥25 individuals. Following planting or natural reseeding, these openings would regenerate into patches of brushy young forest containing ideal conditions for early-successional woodrats. These small patches would then serve as ‘fishing holes’, or dense, self-sustaining populations of woodrats that disperse into the surrounding landscape, providing a food source for foraging spotted owls. While this approach may potentially help support spotted owl populations without compromising fuels reduction goals, effective implementation would benefit from additional research on (1) the effects of these management activities on forest resilience, (2) best practices for the number and distribution of ‘fishing holes’ within a landscape to meet species conservation and forest resilience objectives, and (3) whether smaller patches (≤1 ha) could sustain the same dense, self-sustaining woodrat populations as the ones we evaluated. Further, this approach is less likely to promote spotted owl prey and population health at higher elevations where flying squirrels are the more important prey resource.

Our study also highlights the importance of ephemeral, early-successional habitats in sustaining key prey populations for sensitive species like spotted owls. Unlike late-successional forests, many attributes of early-successional ecosystems depend on time since disturbance and the type, severity, and spatial extent of a disturbance event (Donato et al., 2012; Swanson et al., 2011). These areas undergo structural and compositional changes beginning immediately post-disturbance (Bace et al., 2023), with different species, structures, and ecological processes often dominating throughout different sequences of forest stand development (Swanson et al., 2011). While we did not directly evaluate the effects of temporal heterogeneity, it likely represents an important component of our system as historically variable fire patterns in dry-forest ecosystems produced both spatially and temporally heterogeneous successional processes (McLauchlan et al., 2020). However, in many regions these frequent, low-severity fires have been replaced by large, severe megafires with potential consequences for the abundance and distribution of fire-created early-successional forests at larger spatial scales (Lindenmayer et al., 2019; McLauchlan et al., 2020). In the absence of historical fire regimes, timber harvest within managed landscapes can recurrently create open patches of varying size that regenerate into early-successional forests favored by woodrats, which may explain the high occupancy and abundance rates of woodrats in our study area reported here and in prior studies (Kuntze et al., 2023). Therefore, our findings suggest that promoting multi-scale heterogeneity by continuous, spatiotemporally variable timber harvesting can create and maintain important early-successional ecosystems as part of a diverse landscape.

5. Conclusions

Forest research and management approaches that consider and incorporate ecological complexity and the hierarchical nature of habitat selection can provide valuable insights into how to recreate historically heterogeneous forests and meet biodiversity objectives. While restoring historical disturbance regimes remains a goal in forest ecosystems worldwide (Bullock et al., 2022; Gaines et al., 2022; Steel et al., 2022), it can be challenging – or even impossible – to replicate past conditions and processes (Watts et al., 2020). By grounding restoration policies and practices in the context of the modern environment while prioritizing an understanding of how ecological processes and community composition vary across spatial scales, we can foster consensus and progress among forest management goals.

CRediT authorship contribution statement

M. Zachariah Peery: Writing – review & editing, Writing – original draft, Supervision, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **H. Anu Kramer:** Writing – review & editing, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation. **Brian P. Dotters:** Writing – review & editing, Resources, Project administration, Funding acquisition, Conceptualization. **Kevin N. Roberts:** Writing – review & editing, Resources, Project administration, Funding acquisition, Conceptualization. **John J. Keane:** Writing – review & editing, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Jonathan N. Pauli:** Writing – review & editing, Writing – original draft, Resources, Methodology, Funding acquisition, Conceptualization. **Corbin C. Kuntze:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The USFS Region 5, Sierra Pacific Industries, and USFS Pacific Southwest Research Station funded this work. We are grateful to Byron de Yampert, Zina Lor, and Lily Olmo for their help with data collection in the field, and to William Berigan and Sheila Whitmore for logistical support and spotted owl expertise.

Author contributions

Corbin C. Kuntze, M. Zachariah Peery, Jonathan N. Pauli, H. Anu Kramer, Brian P. Dotters, Kevin N. Roberts, and John J. Keane conceived the ideas and designed the methodology. Corbin C. Kuntze collected the data. Corbin C. Kuntze, H. Anu Kramer, M. Zachariah Peery, and Jonathan N. Pauli analyzed the data. Corbin C. Kuntze and M. Zachariah Peery led the writing of the manuscript, with key input from Jonathan N. Pauli. All authors contributed critically to the drafts and gave final approval for publication.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122412.

Data Availability

Data will be made available on request.

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