

RESEARCH ARTICLE



Structural complexity characterizes fine-scale forest conditions used by Pacific martens

Matthew S. Delheimer¹ | Katie M. Moriarty² |
Holly L. Munro³ | Desiree A. Early⁴ | Keith A. Hamm⁴ |
Rebecca E. Green⁵

¹USDA Forest Service, Pacific Southwest Research Station, 2480 Carson Road, Placerville, CA 95667, USA

²National Council for Air and Stream Improvement, Inc., 2438 NW Professional Drive, Corvallis, OR 97330, USA

³National Council for Air and Stream Improvement, Inc., 180 E Green Street, Athens, GA 30602, USA

⁴Green Diamond Resource Company, PO Box 68, Korb, CA 95550, USA

⁵USDA Forest Service, Pacific Southwest Research Station, 2081 E. Sierra Avenue, Fresno, CA 93710, USA

Correspondence

Matthew S. Delheimer, USDA Forest Service, Pacific Southwest Research Station, 2480 Carson Road, Placerville, CA 95667, USA.
Email: mattdelheimer@gmail.com

Present address

Rebecca E. Green, National Park Service, Sequoia and Kings Canyon National Parks, 47050 Generals Highway, Three Rivers, CA 93271, USA.

Funding information

U.S. Forest Service; U.S. Fish and Wildlife Service, Grant/Award Number: F19PG00107

Abstract

When wildlife species exhibit unexpected associations with vegetation, replication of studies in different locales can illuminate whether patterns of use are consistent or divergent. Our objective was to describe fine-scale forest conditions used by Pacific martens (*Martes caurina*) at 2 study sites in northern California that differed in forest composition and past timber harvest. We identified denning and resting locations of radio-marked martens and sampled structure- and plot-level vegetation using standardized forest inventory methods between 2009–2021. Woody structures used by martens were significantly larger than randomly available structures across types (e.g., live tree, snag, log) and at both study sites. Den and rest structures occurred in areas characterized by higher numbers of logs and snags, lower numbers of live trees and stumps, larger diameter live trees and logs, and greater variation in live tree and log diameter. Features of denning and resting locations were largely consistent across study sites and were generally representative of fine-scale forest heterogeneity and increased structural complexity, conditions that martens have been widely associated with at broader spatial scales (i.e., home range or landscape). The spatial occurrence of denning and resting locations may indicate that fine-scale structural complexity facilitates marten foraging while reducing predation risk. Our work offers timely and directed information that can guide forest management in the context of increased landscape change.

KEYWORDS

boosted 5.0, California, carnivore, decision tree, den, forest structure, *Martes caurina*, Pacific marten

Evaluating wildlife associations with vegetative conditions (e.g., type, composition, structure, successional stage) can guide development of effective forest management strategies, which are critically important as a response to increasing landscape disturbance and change (Jager et al. 2021). Although wildlife species are commonly cast as capable of exploiting a diversity of conditions (i.e., generalists) or constrained to a narrow range of conditions (i.e., specialists; Levins 1968), it may be more appropriate to consider a gradient from generalization to specialization (Peers et al. 2012, Ibarra et al. 2014, Mills et al. 2020). Accordingly, non-stationary relationships or uncharacteristic associations with vegetation have increasingly been described for wildlife species (Shirk et al. 2014, Zuckerberg et al. 2016, Wan et al. 2017, Manzo et al. 2018, Barry et al. 2021). Conditions that appear to be higher quality for a given species can also be strongly dependent on context, such as the spatial or temporal resolution of investigation (Mayor et al. 2009, McGarigal et al. 2016). Given that interpretations can vary, a closer examination may be necessary when animals occupy vegetative conditions that appear to diverge from expectations (Arjo et al. 2003, Kaufman and Kaufman 2015, Karsch et al. 2016, DiMaggio et al. 2018).

Pacific martens (*Martes caurina*) and their close relatives, American martens (*M. americana*), are small carnivores that have been widely associated with specific environmental and vegetative conditions in North America (Buskirk and Powell 1994, Thompson et al. 2012b) but have had less-typical associations identified. For instance, Pacific martens predominantly inhabit mature and relatively undisturbed, high-elevation conifer forests (Spencer et al. 1983, Bull et al. 2005, Martin et al. 2021) that receive substantial amounts of winter snowfall (Zielinski et al. 2017). Accordingly, the range of the Pacific marten closely aligns with upper elevations (>1,000 m) of the Cascade, Sierra Nevada, and southern Rocky Mountains in the western United States (Dawson et al. 2017, Colella et al. 2018). A notable exception is the distribution of the Humboldt marten (*M. c. humboldtensis*), a Pacific marten subspecies (Schwartz et al. 2020), which is in low elevation (0–1,200 m) forests of coastal California and Oregon that receive little to no snowfall (Zielinski et al. 2001). Atypical of conifer forests inhabited by Pacific martens elsewhere, coastal forests inhabited by Humboldt martens can have a substantial hardwood component, and a dense, spatially extensive shrub understory (Slauson et al. 2007; Moriarty et al. 2019, 2021).

Martens have long, thin bodies that are well adapted to living in physically complex forest environments (Krohn et al. 2005, Andruskiw et al. 2008, Martin et al. 2020). Their morphology incurs fitness costs including a relatively high metabolic rate, rapid loss of body heat, and an inability to store substantial fat deposits (Brown and Lasiewski 1972, Worthen and Kilgore 1981, Buskirk and Harlow 1989); thus, martens forage frequently to avoid starvation (Gilbert et al. 2009). Martens occupy colder regions of North America that experience substantial winter precipitation as snow or rain and they must behaviorally thermoregulate to temper heat loss and reduce energetic expenditures (Taylor and Buskirk 1994, Wilbert et al. 2000). To achieve this, male and female martens use insulated sites for resting when not actively foraging, pursuing mates, or maintaining territorial boundaries (Joyce et al. 2017). Similar sites are used by reproductive female martens for denning when rearing their altricial offspring (Delheimer et al. 2021a). Denning and resting locations are typically concealed and secure, offering a necessary degree of protection, as martens are subordinate carnivores that can be killed by a suite of larger predators (Thompson 1994, Bull and Heater 2001, McCann et al. 2010, Woodford et al. 2013, Wilk and Raphael 2018, Martin et al. 2022a).

Cavities and other types of hollows in woody structures such as live and dead trees (snags) provide ideal spaces to seek warmth and safety and are commonly used by martens for denning and resting (Spencer 1987, Bull and Heater 2000, Slauson and Zielinski 2009, Joyce 2013, Delheimer et al. 2021a). Martens have been posited as primarily occupying mature and intact forests, in part because they offer an abundance of large-diameter woody structures suitable for denning or resting (Ruggiero et al. 1998, Slauson and Zielinski 2009). Conversely, younger or regenerating forests (e.g., post timber harvest) are often considered poor quality or suboptimal for long-term

marten persistence, as availability of the types of structures that martens prefer may be relatively limited (Hargis et al. 1999, Payer and Harrison 2003, Fuller and Harrison 2005). Consistent with this premise, Humboldt martens were initially described as predominantly inhabiting mature forest and avoiding regenerating stands (Slauson et al. 2007); however, recent studies suggest Humboldt martens occur in a diversity of successional stages and forest conditions. For instance, Humboldt martens occupy young (<80 year old) coastal dune forests dominated by relatively small diameter trees (Moriarty et al. 2016a, Eriksson et al. 2019, Moriarty et al. 2019) and serpentine forests characterized by sparse trees but extensive shrub cover (Slauson et al. 2007, Gamblin 2019).

Replication of studies in different geographic locales can offer powerful insights when a species occurs across a range of environmental or vegetative conditions (Zanini et al. 2009, Short Bull et al. 2011, Wan et al. 2017). Therefore, our objective was to describe fine-scale forest conditions used by Pacific martens (hereafter, marten) at 2 study sites in northern California that were alike in some respects (e.g., mountainous, predominantly forested) but dissimilar in others (e.g., forest composition, past land use practices). We expected forest conditions used by martens would be consistent, despite apparent differences between study sites, specifically predicting that martens would use rest structures that were significantly larger than structures randomly available on the landscape, and den and rest structures would occur in areas exhibiting features of forest heterogeneity and increased structural complexity. We explore the mechanisms influencing forest associations of martens and consider how our results can provide guidance for supporting marten persistence.

STUDY AREA

We collected data at 2 study sites as part of broader research efforts investigating marten demography (Humboldt site; Delheimer et al. 2021a) and marten space use (Lassen site; Moriarty et al. 2015, 2016b). Both study sites were in northern California and were located approximately 250 km apart (Figure 1). Research at the Humboldt site occurred from 2013–2021 and included 150 km² in the Klamath Mountains. The Humboldt site was occupied by martens in the Humboldt subspecies (Schwartz et al. 2020), which was recently listed as threatened under the federal Endangered Species Act (U.S. Fish and Wildlife Service 2020) and as state endangered in California (California Department of Fish and Wildlife 2019). Elevations ranged from 150–900 m and climate was relatively moderate year-round (average annual temperature = 7–15°C) with substantial rainfall that primarily fell in winter months (average annual precipitation = 100–300 cm; PRISM 2022). Dominant conifer trees included Douglas-fir (*Pseudotsuga menziesii*) and redwood (*Sequoia sempervirens*), while other common conifers included Port Orford cedar (*Chamaecyparis lawsoniana*), western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*). Common hardwood species included chinquapin (*Chrysolepis chrysophylla*), Pacific madrone (*Arbutus menziesii*), and tanoak (*Notholithocarpus densiflora*). Common shrubs included evergreen huckleberry (*Vaccinium ovatum*), Pacific rhododendron (*Rhododendron macrophyllum*), and salal (*Gaultheria shallon*). Land ownership was almost entirely private (>95%) but included small amounts of public ownership (Six Rivers National Forest).

Research at the Lassen site occurred from 2009–2012 and included approximately 250 km² in the southern Cascade Mountains. The Lassen site was occupied by martens in the Sierran subspecies (*M. c. sierrae*; Schwartz et al. 2020). Elevations ranged from 1,700–2,100 m and climate was characterized by warm summers and cold winters (average annual temperature = 3–22 °C), with substantial winter snowfall (average annual precipitation = 50–200 cm; PRISM 2022). Dominant conifer trees included red fir (*Abies magnifica*) and white fir (*A. concolor*). Pines (*Pinus* spp.) were less common but included Jeffrey pine (*P. jeffreyi*), lodgepole pine (*P. contorta*), ponderosa pine (*P. ponderosa*), sugar pine (*P. lambertiana*), and western white pine (*P. monticola*). Hardwood trees (e.g., aspen [*Populus tremuloides*], white alder [*Alnus rhombifolia*]) were uncommon and were restricted to small riparian corridors. Shrubs (e.g., greenleaf manzanita [*Arctostaphylos patula*], mountain whitethorn [*Ceanothus cordulatus*], tobacco brush [*C. velutinus*]) were present but typically not a substantial understory component. Land ownership was almost entirely public (>95%; Lassen National Forest) but included small private inholdings.

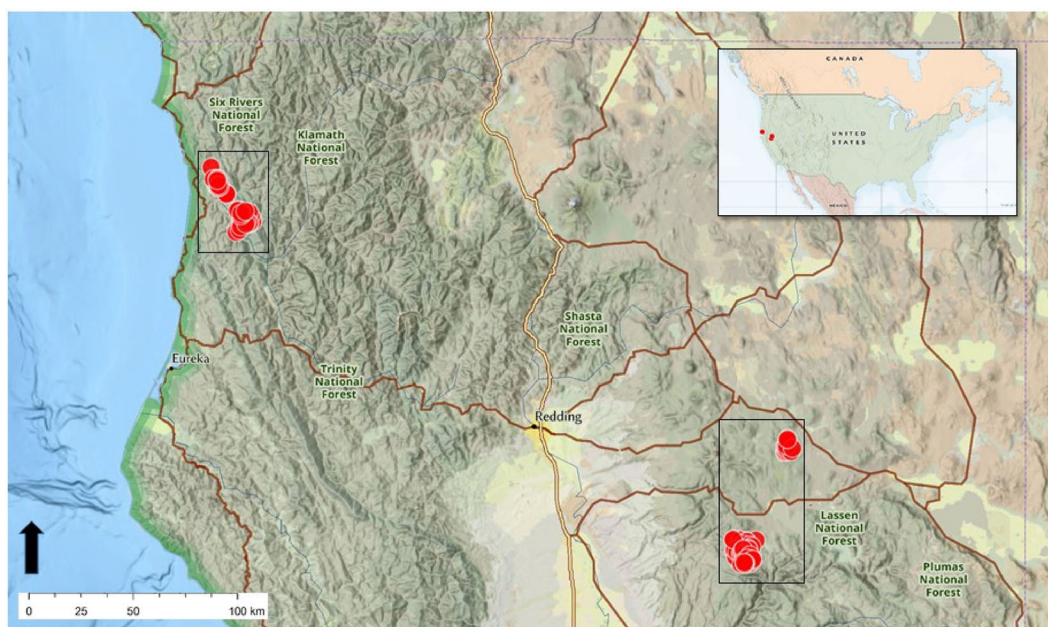


FIGURE 1 Study area including 2 study sites (black boxes) in northern California, USA: Humboldt (upper left) and Lassen (lower right), 2009–2021. We examined use of fine-scale forest conditions used by Pacific martens by measuring structure- and plot-level forest vegetation features at used denning and resting locations and randomly available locations (red circles). Map indicates major cities and towns in the region (black dots), interstates and highways (solid yellow or brown lines), and state boundaries (dashed purple lines).

Past land use practices differed between the Humboldt and Lassen sites, particularly with respect to timber harvest intensity and extent. The Humboldt site was managed for commercial timber production beginning in the 1950s and most stands experienced one or more harvest entries during the last 70 years (Hamm et al. 2012). Earlier harvest practices were typified by a form of selective logging where most of the valuable overstory conifer volume was removed, while some seed trees and trees with low merchantability (e.g., hardwoods, defective conifers) were retained (O'Dell 1996). Clearcutting became a common harvest practice in the 1970s, although changing state forest practice regulations in the 1990s and species' listings prompted increased riparian protection and upland tree retention (Diller and Thome 1999, Hamm et al. 2012). The Lassen site was managed for multiple uses that were not exclusive to timber production (e.g., recreation, livestock grazing) and harvest did not occur in all stands (U.S. Department of Agriculture [USDA] Forest Service 2011). Harvest began in the 1940s and practices were typified by high-grading or diameter-limit cutting, which involved preferentially removing only the largest and most commercially valuable trees (Russell-Roy et al. 2014). Harvest was limited in scope following the 1980s, occurring in small areas that were managed for fuels reduction (e.g., via mechanical thinning; USDA Forest Service 2011).

METHODS

Animal capture and tracking

We captured martens using modified wire mesh live traps (model 106; Tomahawk Live Traps, Hazelhurst, WI, USA). We anesthetized martens via intramuscular injection of a ketamine and midazolam mixture (Mortenson and Moriarty 2015). We recorded marten sex, mass, and other morphological features (e.g., body length) and estimated

age class (young-of-the-year or juvenile, subadult, adult; Jonkel and Weckwerth 1963). We removed a vestigial upper premolar tooth to verify age via cementum annuli analysis (Poole et al. 1994). We fit martens with a 28–30-g very high frequency radio-collar (model M1800, Advanced Telemetry Systems, Isanti, MI, USA; model MI-2, Holohil Systems LTD., Carp, Ontario, Canada) that represented 3–5% of body weight (Sikes et al. 2016).

We tracked radio-marked martens using ground-based telemetry and searched for each marten on multiple occasions each week (typically ≥ 2 search days) to assess their status (alive, dead, missing). We estimated marten positions at least once per week using standardized telemetry methods, which typically consisted of a triangulated set of ≥ 3 compass bearings (Thompson et al. 2012a). When telemetry signals indicated that a marten was inactive, we used homing techniques to track martens on foot (Green et al. 2017). We identified the specific structure (rest or den) that each marten was occupying via a combination of visual observation, vocalizations, sign (e.g., tracks), or strength of the telemetry signal. When possible, we identified the marten's precise position (e.g., microsite) within a rest or den structure (Joyce et al. 2017, Tweedy et al. 2019).

Structure- and plot-level sampling

We sampled vegetation at marten denning and resting locations, which we generally defined as including both the specific den or rest structure and its immediate surroundings. We categorized woody structures used for denning (i.e., seasonally by parturient female martens for raising offspring) and resting (i.e., by female and male martens year-round) by structural type, measuring diameter-at-breast height (cm) of live trees and snags and maximum diameter of logs. We distinguished dens from rest structures by verifying the presence of dependent kits via motion-sensitive camera monitoring (Delheimer et al. 2021a). Dead trees were a minimum height of 2 m to be considered snags. We identified woody structures to tree species whenever possible but minimally classified them as conifer or hardwood if we could not determine species. Non-woody structure types included slash piles (accumulations of small diameter trees that were felled but not removed during timber harvest activities), burrows (either under-ground or under-snow locations), and rock piles (Table 1).

We compared rest structure sizes to randomly available structure sizes by averaging all structures across random plots, using a structure diameter threshold of ≥ 30 cm. We considered comparisons for structure types that were used ≥ 5 times at a given site (Humboldt: live trees, logs, and snags; Lassen: live trees and snags), assuming no difference in structure use by female versus male martens (Tweedy et al. 2019). We did not conduct den structure size comparisons, as den structure sizes at the Humboldt site have been summarized elsewhere (Delheimer et al. 2021a), while den structures were not identified at the Lassen site. At the Humboldt site, we separated live trees by conifer and hardwood, given that conifers (e.g., redwoods) can achieve much larger diameters than hardwoods. We compared conifers only for logs and snags at the Humboldt site, as hardwoods were not used (logs) or were rarely used (snags) in these structure types. Rest structures did not occur in hardwoods at the Lassen site. We used non-parametric Mann-Whitney *U* tests (significance level $P \leq 0.05$) for statistical analyses because sample sizes were small for used structures and we were unable to transform non-normally distributed data.

We conducted plot-level sampling at each study site to characterize overstory vegetation, understory vegetation, and coarse woody debris at used denning and resting locations (specifically, the area surrounding den

TABLE 1 Summary of rest structure types used by Pacific martens at 2 study sites in northern California, USA, 2009–2021.

	Live tree	Snag	Log	Stump	Rock pile	Slash pile	Burrow
Humboldt	59	17	6	1	3	8	0
Lassen	7	18	0	3	2	0	8

and rest structures) and randomly generated locations (Manly et al. 2002, Johnson et al. 2006). We used a combination of fixed- and variable-radius plots, with most plot sampling methods identical or equivalent between the Humboldt and Lassen sites. We specified that each random location had to be ≥ 200 m from used locations and other random locations to limit spatial autocorrelation but within the radius of a male marten territory (approximately 400–800 ha, depending on the study site; Moriarty et al. 2017) to address assumptions of availability. We centered plot sampling on the rest or den structure at used locations. At random locations, we centered plot sampling on a structure (≥ 30 cm diameter) that was as close as possible to our randomly generated point. We used a variable-radius plot to sample live trees, as variable-radius plots are typically preferable to fixed-radius plots for inventories in stands that are less dense or composed of larger-diameter trees (Stage and Rennie 1994, Packard and Radtke 2007). We measured diameter-at-breast height of all live trees within the variable-radius plot, determined via a 20-factor basal area prism positioned at plot center. We established 4 line transects (Humboldt: 12.5 m length; Lassen: 15 m length), each radiating from plot center and 90° apart, measuring the distance (≥ 0.1 -m increments) along each transect that was intercepted by shrub cover. Line transects acted as radii for circular fixed-area plots where we conducted woody structure counts (Humboldt: 0.2 ha; Lassen: 0.09 ha), measuring all snags, stumps, and logs > 30 cm (diameter-at-breast height or maximum diameter) within the plot. We multiplied woody structure counts at Lassen by 2.22 to adjust for the smaller fixed area plot size, which allowed for comparisons between sites.

We conducted canopy measurements using a spherical densiometer at the Humboldt site and a moosehorn at the Lassen site. Spherical densiometers produce consistently higher canopy estimates than moosehorns because of an increased angle of view (Fiala et al. 2006) and as such, we considered our estimates to be incompatible between sites. Remotely sensed canopy estimates can be highly accurate (Smith et al. 2009); thus, we chose to incorporate canopy cover data downloaded from the California Forest Observatory (<https://forestobservatory.com/>, accessed 1 Mar 2022; Salo Sciences, San Francisco, CA, USA). We used 2016 canopy cover data, given that neither study site experienced disturbance (e.g., timber harvest or fire) within the timeframe of our study that would affect canopy cover and assuming that canopy cover had otherwise experienced minimal change during the study period. We averaged canopy cover (10-m pixel resolution) across a 25-m-radius buffer around each point (i.e., the size of a fixed area plot at the Humboldt site) using a moving window analysis in ArcGIS (version 10.7.1, Esri, Redlands, CA, USA).

Plot-level modeling

For our analysis, we considered marten presence (i.e., used denning or resting locations; $n = 158$) or pseudo-absence (i.e., random locations; $n = 105$) as our response (Barbet-Massin et al. 2012). We grouped all used locations (female denning, female resting, and male resting) because our sample size was small for denning locations ($n = 26$) and we assumed that individual female and male martens did not use locations differentially (Raphael and Jones 1997, Tweedy et al. 2019). We compared fine-scale forest features that we identified as potentially influential to marten denning or resting (Porter et al. 2005, Godbout and Ouellet 2010, Sanders et al. 2017, Tweedy et al. 2019). Features included plot-level woody structure counts (live tree, log, snag, and stump), average woody structure sizes, variation in woody structure sizes (standard deviation), percent shrub cover, and percent canopy cover. We included a study area variable to help control for potential differences between sites (e.g., forest composition, management history). We did not consider terrain (e.g., elevation, slope) or climatic variables (e.g., precipitation, temperature) because we were specifically interested in examining features that are alterable or targetable within a forest management context.

We used decision trees to evaluate fine-scale use of marten denning and resting locations. Decision trees and other supervised machine learning approaches (e.g., random forest) attempt to model the relationship between a response and its predictors (Breiman 2001), offer powerful alternatives to traditional ecological modeling approaches (e.g., generalized linear models; De'ath and Fabricius 2000, Olden et al. 2008), and have been

increasingly applied in investigations of wildlife habitat use (Han et al. 2017, Mi et al. 2017, Cushman and Wasserman 2018, Carroll et al. 2021, Rather et al. 2021). We built decision trees by incorporating plot-level data into a boosted C5.0 algorithm (Quinlan 1993), which we chose because of its nominal sensitivity to multicollinearity and unbalanced data, ability to manage missing values, and relative ease of interpretation (Guilherme et al. 2018, Szilassi et al. 2019, Moeinaddini et al. 2020, Tanyu et al. 2021, da Silveira et al. 2022). Allowing for missing values was particularly important in selecting our modeling approach, as calculation of some values in our dataset was contingent on another value being non-zero (e.g., we could not calculate average log diameter in plots that did not contain any logs).

We used the boosted C5.0 algorithm to build decision trees via recursive partitioning, which split data into groups based on features (i.e., subsets of data) that provided maximum information gain (Strobl et al. 2009). Each decision tree started at a root node and the algorithm determined which feature the tree split on at intermediate nodes by using entropy to measure purity, whereby groups contained less diverse classes until they only contained one class (i.e., complete purity). Resultant information gain was calculated by subtracting the entropy after the split (S_2) from the entropy before the split (S_1). Higher information gain values indicated more pure groups and determined the rule that was used for each split. Splits continued until the samples could not be split further, ending in terminal nodes that represented groups with a single class. We calculated entropy before the split (S_1) using Equation 1:

$$Entropy(S_1) = \sum_{i=1}^c -p_i \log_2(p_i), \quad (1)$$

where p_i was the proportion of samples per class (c) at level i . We calculated entropy for each partition after the split, extending the above equation by summing the entropy of each partition (n) but weighting each partition by the number of samples in that partition (w_i):

$$Entropy(S_2) = \sum_{i=1}^n w_i Entropy(p_i). \quad (2)$$

Feature importance within a decision tree was indicated by the divergent node where a feature split (i.e., an earlier split represented a feature predicted to be more important). We provided an index of importance calculated as the percentage of samples that fell into terminal nodes after that split (Bui et al. 2006).

We separated the dataset into random iterations of training (90%) and test data (10%) and trained the boosted C5.0 algorithm using 100 decision trees. The algorithm had 2 main meta parameters, including number of trees and minimum number of samples (MinCases) placed in at least 2 splits (Elsayad et al. 2020). We used early stopping to prevent model overfitting (Caruana et al. 2000, Jabbar and Khan 2015), which reduced the final number of trees. The MinCases meta parameter indirectly controlled the depth of the decision tree and as this meta parameter increased, tree complexity decreased. We iteratively tuned MinCases to improve model accuracy (Abonyi et al. 2003, Stiglic et al. 2012), starting with a value of 2 until no decreases in error were observed, which resulted in a final MinCases of 8. We calculated relative importance of predictor variables by averaging across all trees the number of times that a feature was selected for splitting, weighted by the squared improvement to the model resulting from each split (Friedman and Meulman 2003). To evaluate variable performance, we interpreted partial dependence plots and confidence intervals (lower and upper 95%) of the 10 most important features. We calculated confidence intervals using 50 bootstrap replicates (Cafri and Bailey 2016).

Because of class imbalance, we used both accuracy and balanced accuracy to assess overall model performance (Bekkar et al. 2013), but we also included other common performance metrics (Kappa, sensitivity, specificity, and McNemar's test) to clarify model interpretation. Accuracy is the ability of the model to correctly classify positive or negative observations (i.e., marten presence or pseudo-absence), calculated as the number of positive observations divided by the total number of observations. Kappa compares the ability of the model to correctly classify observations (accuracy), relative to the ability of a random classifier (i.e., expected accuracy). Balanced accuracy

averages sensitivity and specificity, where sensitivity is the proportion of positive observations correctly classified by the model (true positives) and specificity is the proportion of negative observations correctly classified by the model (true negatives). McNemar's test compares whether the proportion of positive observations incorrectly classified by the model (false positives) and negative observations incorrectly classified by the model (false negatives) are different. For accuracy, Kappa, sensitivity, specificity, and balanced accuracy metrics, a value closer to 1 generally indicates improved model performance. McNemar's test represents a P -value, where $P > 0.05$ indicates that there is not a significant difference between proportion of false positives and false negatives (i.e., the model performed similarly when classifying false observations).

We performed all analyses in program R (version 4.0.5; R Core Team 2021). We used packages including readxl (Wickham and Bryan 2022) and dplyr (Wickham et al. 2022) for data preparation and exploration; C50 (Kuhn and Quinlan 2022) and caret (Kuhn 2022) for data analyses and model evaluation; and pdp (Greenwell 2017), vip (Greenwell and Boehmke 2020), and ggthemes (Arnold 2021) for model explanation and visualization.

RESULTS

We identified 94 marten rest structures ($n = 66$ female, $n = 28$ male) used at the Humboldt site and 38 rest structures ($n = 12$ female, $n = 26$ male) used at the Lassen site. At both Humboldt and Lassen, martens most commonly rested in woody structures (88% [$n = 83$] and 74% [$n = 28$] of structures, respectively; Table 1). At the Humboldt site, live conifer tree (83.1 ± 53.4 cm [$\bar{x} \pm SD$]; $U' = 2,099$, $P = 0.008$) and live hardwood tree rest structures (74.0 ± 25.0 cm; $U' = 1,418$, $P < 0.001$) were larger diameter than randomly available structures, as were conifer snag (131.2 ± 50.5 cm; $U' = 116$, $P < 0.001$) and conifer log rest structures (122.2 ± 34.1 cm; $U' = 117$, $P < 0.001$; Figure 2). At the Lassen site, live conifer tree (88.5 ± 32.1 cm; $U' = 651$, $P = 0.019$) and conifer snag rest structures (96.4 ± 40.5 cm; $U' = 438$, $P < 0.001$) were larger diameter than randomly available structures (Figure 3).

We conducted sampling at 158 used plots and 105 random plots, including 120 used plots ($n = 92$ female, $n = 28$ male) and 60 random plots at the Humboldt site and 38 used plots ($n = 12$ female, $n = 26$ male) and 45 random plots at the Lassen site (Figure 1). The boosted C5.0 algorithm performed well on plot-level training (93.6% accuracy; 92.9% balanced accuracy) and test data (89.7% accuracy; 87.5% balanced accuracy; Table 2). Other

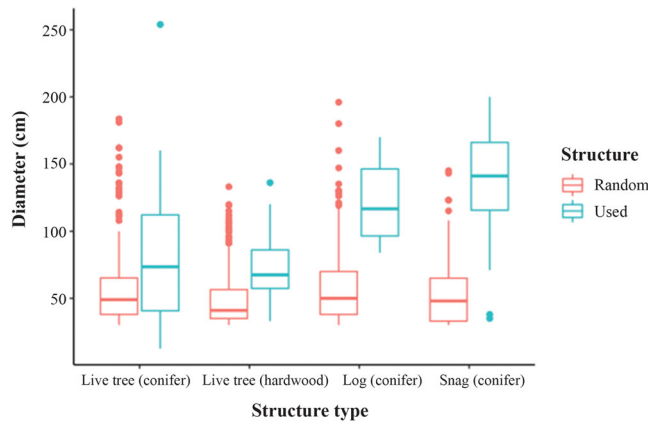


FIGURE 2 Size distribution of used rest structures (green) of Pacific martens and randomly available structures (red) at the Humboldt study site in northern California, USA, 2013–2021. We split our data to show diameters of live conifer trees, live hardwood trees, conifer logs, and conifer snags. Boxplots indicate median values (thick horizontal lines) and boxes bound 25% and 75% quartiles, while dots represent extreme values.

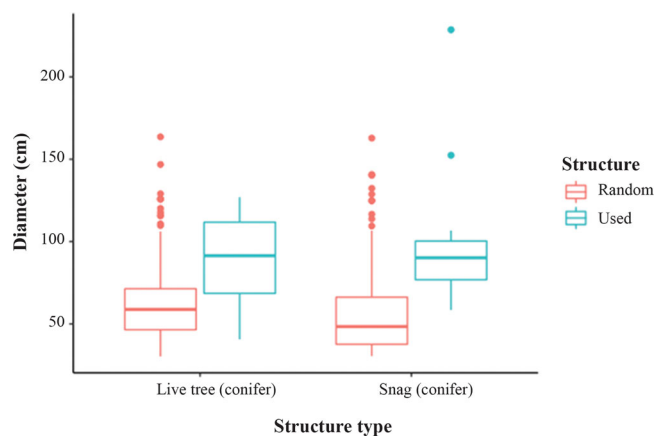


FIGURE 3 Size distribution of used rest structures (green) of Pacific martens and randomly available structures (red) at the Lassen study site in northern California, USA, 2009–2013. We split our data to show diameters (cm) of live conifer trees and conifer snags. Boxplots indicate median values (thick horizontal lines) and boxes bound 25% and 75% quartiles, while dots represent extreme values.

TABLE 2 Boosted C5.0 model performance of training and test data used to examine plot-level forest conditions at denning and resting locations of Pacific martens at 2 study sites in northern California, USA, 2009–2021.

Metric	Training data	Test data
Accuracy (95% CI)	0.936 (0.897, 0.964)	0.897 (0.727, 0.978)
Kappa	0.865	0.779
Sensitivity	0.965	1.000
Specificity	0.893	0.750
Balanced accuracy	0.929	0.875
McNemar's test	0.302	0.248

metrics used to evaluate training and test data suggested little to no overfitting of models (Table 2). Error associated with individual decision trees ($n = 71$) within the ensemble C5.0 algorithm averaged 28.3% (range = 18.8–52.1%).

All plot-level forest structural features were associated with den or rest use by martens (Figure 4), although features had varying levels of predicted importance. Highest-ranked features included canopy cover, number of live trees, number of logs, number of snags, and number of stumps (each feature present in >99% of decision trees), while snag diameter (present in 47.9% of decision trees) and variation in snag diameter (present in 46.6% of decision trees) were the lowest ranked features (Figure 4). Shrub cover was the only feature that was not consistently important across study sites, having a nominal importance for Lassen and only used in terminal nodes (primarily at Humboldt) following a split by site. The decision tree with the lowest error (18.8%; accuracy 81.2%) included number of live trees, number of logs, number of stumps, average log diameter, and average snag diameter (Figure 5; Table 3).

At the plot level, marten use had a positive relationship with number of logs and snags, diameter of live trees and logs, and canopy cover, and a negative relationship with number of trees and stumps (Figure 6). Probability of use increased strongly with increasing number of logs, peaking at an average of 18 logs/plot and remaining constant afterwards (Figure 6). Probability of use similarly increased with increasing number of snags, with probability being

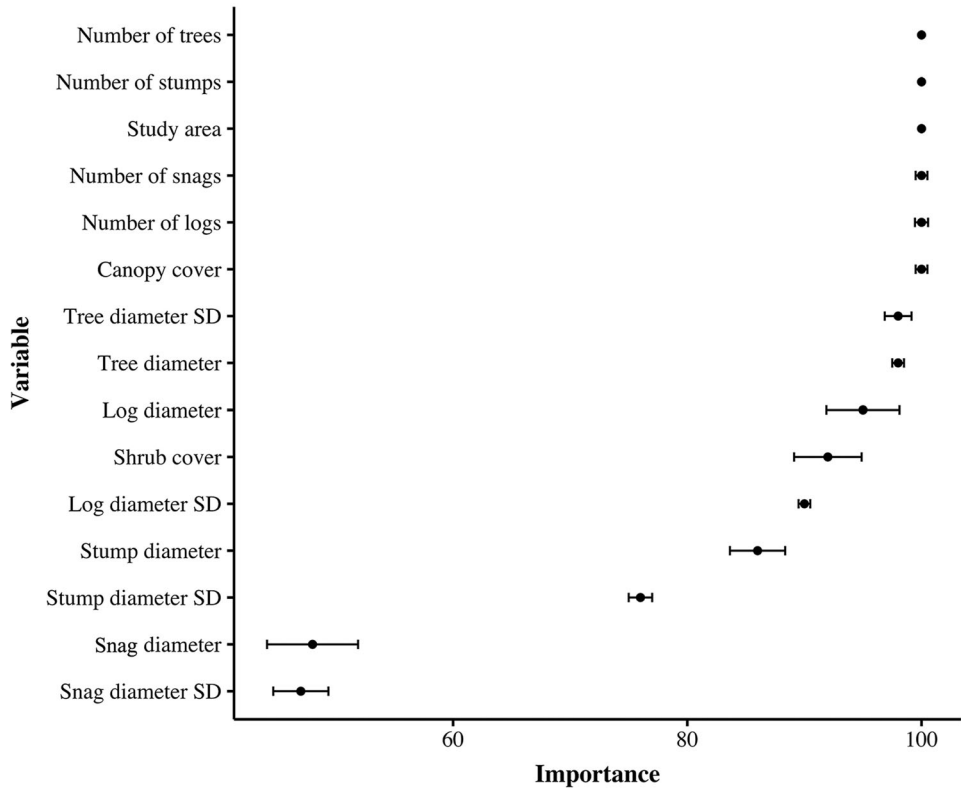


FIGURE 4 Relative importance of plot-level features at denning and resting locations of Pacific martens at 2 study sites in northern California, 2009–2021. Features included woody structure counts (numbers of live trees, logs, snags, or stumps), average woody structure diameters (cm), variation in woody structure diameters (standard deviation), canopy cover (%), and shrub cover (%). We included a study area variable to help control for potential differences between the Humboldt and Lassen study sites (e.g., forest composition, management history). We derived feature importance from boosted C5.0 decision trees, with importance calculated based on the percentage of samples that fell into terminal nodes. Whiskers indicate standard error of each feature.

relatively high in plots with ≥ 1 snag and peaking at an average of 4 snags/plot (Figure 6). Used plots had larger diameter trees (average >40 cm) and larger diameter logs (average 45–55 cm) compared to random plots (Figure 6). Probability of use decreased with increasing number of live trees, up to 12 trees/plot, after which it remained constant (Figure 6). Probability of use also decreased with increasing number of stumps, with a relatively strong decrease at >7 stumps/plot (Figure 6). Used plots had greater variation in diameter of live trees and logs compared to random plots (Figure 6). Probability of use increased with increasing canopy cover, although the relationship was relatively weak and had wide confidence intervals (Figure 6). Shrub cover only had an effect at the Humboldt site, where probability of use was low only at low shrub cover levels ($<20\%$; Figure 7).

DISCUSSION

Our research indicates that fine-scale forest conditions of marten denning and resting locations were largely similar across study sites that were not entirely analogous, as martens consistently used large diameter woody structures (e.g., live trees, snags) that were surrounded by specific forest attributes (e.g., greater numbers of larger diameter

C5.0 Tree 7
Overall error = 18.8%
Accuracy = 81.2%

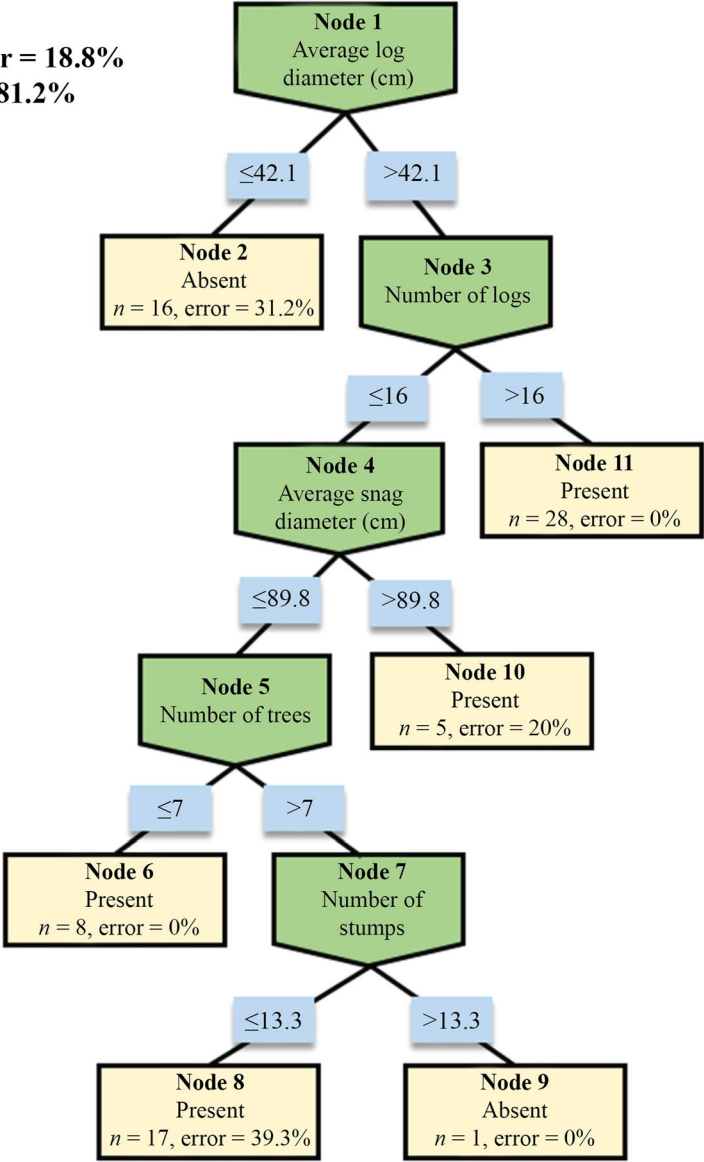


FIGURE 5 Example of a decision tree (tree 7 of 71) used to examine plot-level features at denning and resting locations of Pacific martens at 2 study sites in northern California, USA, 2009–2021. We present the tree with the lowest error (18.8%) produced by the boosted C5.0 model. The root node and intermediate nodes are green, while terminal nodes are light tan. Blue boxes indicate how the data were split at a given feature and node. Terminal nodes indicate whether a marten was predicted to be present or absent, number of observations falling in that node, and the error associated with terminal node predictions; see Lin et al. (2006) for interpretation of individual decision trees.

logs), despite differences between sites in forest composition and past land use practices. Performance of decision tree models in discriminating between used and randomly available plots supports their utility, as decision trees and other supervised machine learning methods are well-suited to handle ecological datasets that are often imperfect (De'ath 2007, Elith et al. 2008, Olden et al. 2008). Compatible data collection methodologies allowed us to leverage research from both study sites by incorporating data into a single model framework, illustrating the value of

TABLE 3 Summary values ($\bar{x} \pm \text{SD}$) for plot-level features at used denning and resting locations of Pacific martens and randomly available locations at 2 study sites in northern California, USA, 2009–2021. Features are averaged by plot type (used or random) at each study site (Humboldt or Lassen). Woody structure counts (number of logs, snags, and stumps) at Lassen are adjusted to account for differences in fixed plot sizes between study sites. Diameter measurements are in centimeters, while cover measurements represent percentages.

Feature	Humboldt		Lassen	
	Used (n = 120)	Random (n = 60)	Used (n = 38)	Random (n = 45)
Number of live trees	9.8 ± 5.5	12.5 ± 4.8	11.8 ± 5.2	9.6 ± 5.4
Live tree diameter	39.4 ± 30.4	35.2 ± 24.8	53.4 ± 29.9	56.9 ± 23.0
Number of logs	18.5 ± 11.7	7.1 ± 5.3	12.3 ± 7.3	7.9 ± 7.5
Log diameter	56.4 ± 24.9	56.4 ± 24.8	56.5 ± 27.4	45.4 ± 20.9
Number of snags	2.3 ± 2.3	1.1 ± 1.9	5.0 ± 4.7	3.8 ± 4.8
Snag diameter	56.8 ± 35.6	55.3 ± 28.7	64.5 ± 32.4	49.3 ± 15.1
Number of stumps	8.0 ± 6.5	6.3 ± 5.6	4.5 ± 6.2	14.1 ± 15.0
Stump diameter	90.8 ± 43.8	84.6 ± 34.5	74.0 ± 41.4	57.0 ± 27.2
Canopy cover	88.0 ± 8.2	86.3 ± 9.2	55.5 ± 11.6	46.7 ± 18.5
Shrub cover	43.9 ± 25.3	34.3 ± 29.0	3.6 ± 6.4	6.2 ± 10.4

replication in accumulating evidence and strengthening inference (Johnson 2002). This approach is particularly important for relatively rare species such as martens that may have large knowledge gaps and require substantial effort to study (Martin et al. 2022b).

Martens exhibited strong structure-level selection, consistent with previous evidence that woody structures used by martens are larger in diameter than those otherwise available on the landscape (Martin and Barrett 1991, Raphael and Jones 1997, Sanders et al. 2017, Tweedy et al. 2019). Given marten ecology, our finding that rest structures were large and relatively uncommon is intuitive, yet the relevance of this is still worth considering. Live trees and snags comprised the majority of rest structures at both study sites, and although it was often difficult to verify precise positions of martens within trees and snags, many if not most were likely in cavities (Delheimer et al. 2021a). Growth to a sufficient size, which can take decades to centuries (Hennon and Mulvey 2014), is prerequisite for a tree bole to develop a cavity or other hollow that is large enough to accommodate a marten. The cavity development process itself can similarly require substantial amounts of time (Manion 1981, Bull et al. 1997), yet not all older or larger trees will contain cavities and not all cavities will fit a marten. The value of large, decadent trees as forest features is thus implicitly high given their inherent rarity and importance to meeting marten life-history needs (e.g., parturition, predator avoidance, thermoregulation; Joyce 2013; Wilk et al. 2018; Delheimer et al. 2019, 2021a; Velandier 2022).

While martens selected individual structures with relatively apparent attributes (e.g., large size), it is reasonable to presume that the immediate environment around structures is similarly important. As relatively small carnivores with high energetic requirements and numerous potential predators, martens occupy a tenuous trophic position of having to secure enough to eat while avoiding being eaten (Martin et al. 2020), a position that may be particularly precarious for reproductive female martens that must meet their own energetic needs and those of their dependent offspring (Delheimer et al. 2021b). Given this, we posit that den and rest structures should primarily occur where martens can successfully find and kill prey, while avoiding becoming prey themselves. Using rest and den structures in areas characterized by heterogeneous and structurally complex forest conditions, which martens have been widely associated with at broader spatial scales (e.g., home range to landscape; Payer and Harrison 2003, Godbout and Ouellet 2010, Shirk et al. 2014, Tweedy et al. 2019, Martin et al. 2021), should offer opportunities to improve

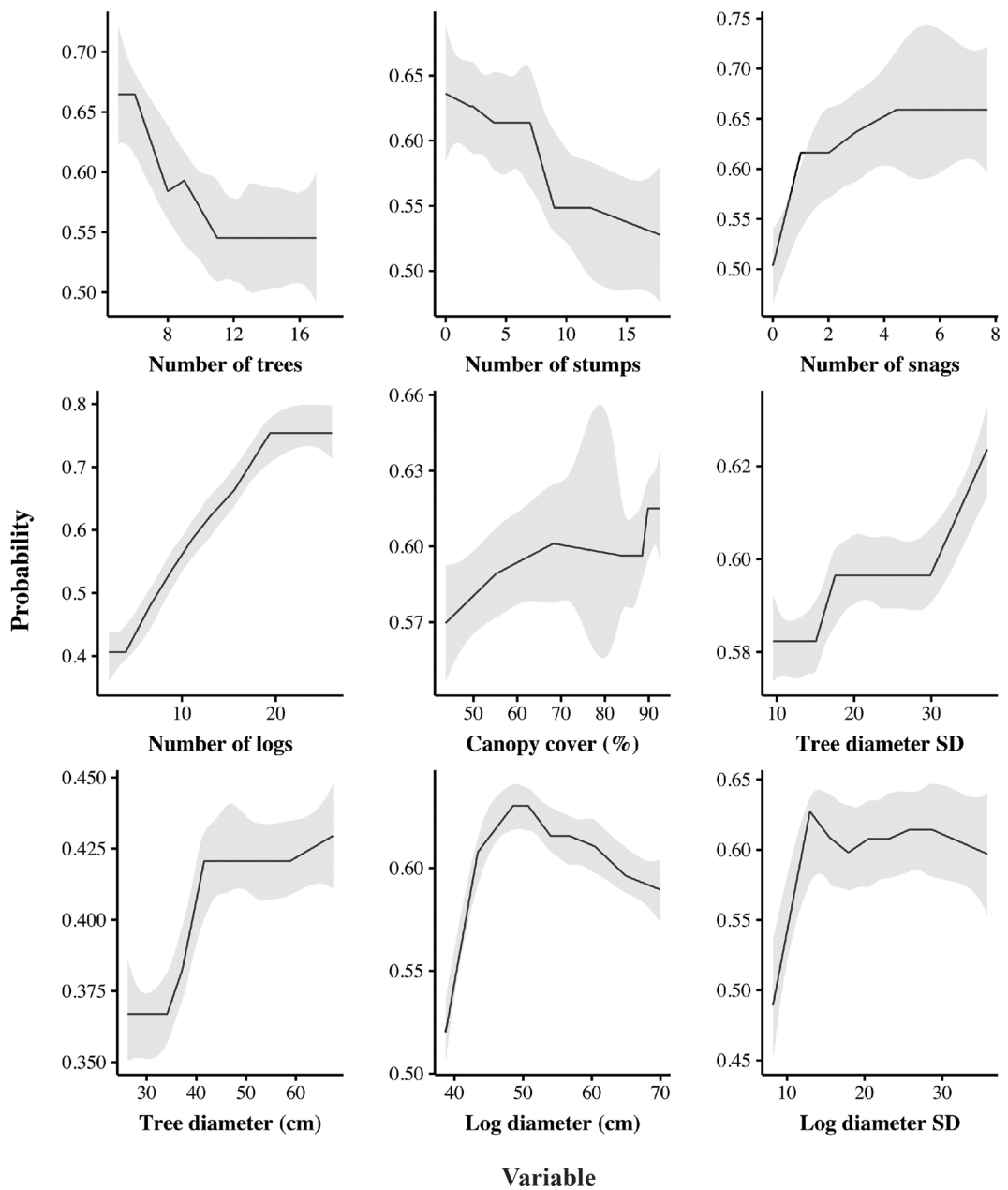


FIGURE 6 Partial dependence plots ($\pm 95\%$ CIs; grey shading) of plot-level features at denning and resting locations of Pacific martens at 2 study sites in northern California, USA, 2009–2021. We present the most predictive forest structural features as identified by the boosted C5.0 model. Note that probability of use (y-axis) changes scales between plots.

foraging and reduce predation risk while minimizing the amount of energy expended in the process (Moriarty et al. 2015).

We interpreted many plot-level features as representative of forest heterogeneity and structural complexity. For instance, large logs and other coarse woody debris create horizontal complexity that facilitates efficient marten foraging (Andruskiw et al. 2008) but also provide martens with escape cover; accordingly, greater numbers of

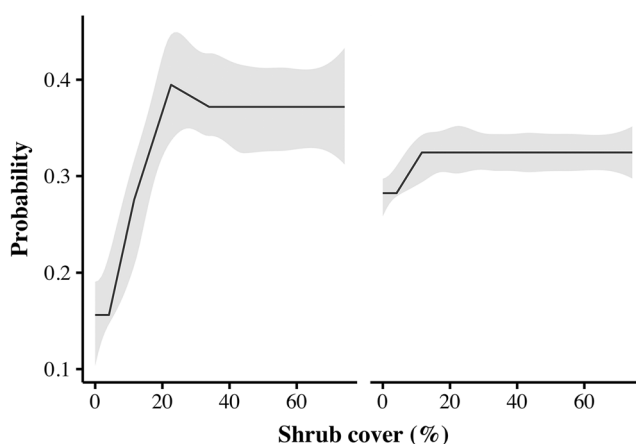


FIGURE 7 Partial dependence plots ($\pm 95\%$ CIs; grey shading) for shrub cover (%) at denning and resting locations of Pacific martens at 2 study sites in northern California, USA, 2009–2021. We present predictions from the boosted C5.0 model. We specifically differentiated shrub cover between study sites (Humboldt, left; Lassen, right), as it was the only feature not consistently important at both sites.

relatively large diameter logs was a primary feature of used plots in our work (Figure 4). Small mammals that are common in marten diets (e.g., voles [*Myodes* and *Microtus* spp.], deer mice [*Peromyscus maniculatus*]; Slauson and Zielinski 2017, Wilk and Raphael 2017, Eriksson et al. 2019) are often associated with coarse woody debris (Ucitel et al. 2003, Pauli et al. 2006, Fauteux et al. 2012, Sullivan et al. 2017), from which martens appear to acquire sensory cues that aid in locating prey (Corn and Raphael 1992, Andruskiw et al. 2008). Other prey items, such as Douglas' squirrel (*Tamiasciurus douglasii*), build and occupy cone caches in large logs where they may be susceptible to marten predation (Zielinski et al. 1983, Ruggiero et al. 1998). In winter months, logs intercept snow and form interstitial spaces that martens exploit to hunt in the subnivium (Corn and Raphael 1992, Sherburne and Bissonette 1994).

Vertical forest structural complexity should be collectively created by many of our predicted plot-level features and may function primarily to alleviate marten mortality risk from larger-bodied terrestrial and avian carnivores (Godbout and Ouellet 2010, Cheveau et al. 2013, Smith et al. 2022b). For instance, presence alone of larger trees or snags provides martens with options for escape from primary terrestrial predators (e.g., bobcat [*Lynx rufus*], coyote [*Canis latrans*]; Martin et al. 2022) that are poorly suited to climbing (Hodgman et al. 1997). Consistent with our findings, martens have been commonly described as inhabiting forests with relatively high amounts of canopy cover (Cushman et al. 2011, Shirk et al. 2014, Tweedy et al. 2019), which offers overhead protection from raptors (e.g., northern goshawk [*Accipiter gentilis*], great horned owl [*Bubo virginianus*], peregrine falcon [*Falco peregrinus*]) that have been documented to kill martens (Thompson 1994, Bull and Heater 2001, McCann et al. 2010). Nonetheless, canopy heterogeneity is likely to be as important as canopy cover for martens, given that some raptors (e.g., goshawks) are adept at hunting in complex environments (Beier and Drennan 1997). Marten den and rest structures occurred in areas with less trees that were larger and more variable in size compared to trees in random plots (Figure 6), which we interpreted as creating multi-layered, heterogeneous canopies that should optimize marten opportunities for avoidance and escape from predators.

A high amount of shrub cover was common at the Humboldt study site only (Figure 7), consistent with the premise that shrubs are a primary feature of forests inhabited by Humboldt martens (Moriarty et al. 2021). Extensive shrub cover is atypical of marten-inhabited forests elsewhere in North America, which are generally located at higher latitudes or higher elevations that have deep and persistent winter snowpacks, such as at our Lassen study site. Snow provides heterogeneous conditions for martens that can only be created by forest structure

in snow-free periods (Smith et al. 2022b) and marten morphology is highly adapted to snow (Krohn et al. 2005). Snow simultaneously limits the presence of larger carnivores that lack similar morphological adaptations (Martin et al. 2021, Smith et al. 2022b) while also facilitating improved hunting efficiency of martens during an energetically demanding time of year (Buskirk and Harlow 1989, Gilbert et al. 2009, Martin et al. 2020). Given the prevalence of shrubs and absence of snow in regions where Humboldt martens occur, we posit that shrub cover serves proxy functions for snow in areas where snow cover is inconsistent or not present. Dense shrubs likely present an obstacle to movement by larger-bodied predators and shrubs should both directly and indirectly subsidize marten diets, given that martens consume prey (e.g., small mammals, birds) that eat berries and mast, while also consuming berries themselves (Eriksson et al. 2019). Lacking the seasonal heterogeneity that snow provides, forest structural complexity—including that created by shrubs—is likely of particular importance for Humboldt martens.

Our study focused on marten associations with forest conditions at a fine spatial resolution and we acknowledge that inference beyond this scale is limited. Importance of scale to understanding habitat use has been widely indicated (Wiens 1989, Mayor et al. 2009) and specifically noted for martens (Shirk et al. 2014, Tweedy et al. 2019). Investigations at multiple or optimized scales can be informative and their utility is clear for some applications (e.g., modeling species' distributions; Vergara et al. 2016, Macdonald et al. 2019, Hallman and Robinson 2020), as patterns can be apparent at one scale but not necessarily at another (Jackson and Fahrig 2015, McGarigal et al. 2016). Such efforts are either reliant on data from remotely sensed sources (e.g., satellite imagery, aerial photography, Light Detection and Ranging [LiDAR]) or data that has been broadly extrapolated from on-the-ground measurements. While remotely sensed estimates can be highly accurate for some overstory forest features (e.g., canopy cover, canopy height), remote sensing typically performs poorly at capturing understory components (e.g., logs, shrubs; Hall et al. 2005), although LiDAR shows promise in overcoming this limitation (Joyce et al. 2019, Jarron et al. 2020, Smith et al. 2022a).

Despite potential advances, field-based data such as ours remains invaluable to characterize fine-scale forest conditions (Zellweger et al. 2014). Indeed, we were specifically interested in providing information at a scale that is relevant to contemporary forest management, particularly in light of management options being considered to reduce the escalating threat of large, severe wildfires to coniferous forests of western North America (Abatzoglou and Williams 2016, Hagmann et al. 2021). For instance, fuels reduction treatments (e.g., mechanical thinning, prescribed fire) are proactive forest management practices that can mediate wildfire behavior (Stephens et al. 2012) and increasing application of treatments is likely (Hessburg et al. 2021, North et al. 2021, Prichard et al. 2021). While treatments are intended to bolster long-term forest resilience, their widespread application may result in shorter-term degradation of conditions for martens by simplifying forest structure, which can alter space use and movement patterns (Godbout and Ouellet 2010; Moriarty et al. 2015, 2016b). Maintenance of biodiversity is fundamental to the concept of forest resilience; thus, effective forest management will address the requirements of vulnerable species, such as martens, to fully realize objectives (Cantarello et al. 2017, Messier et al. 2019, Nikinmaa et al. 2020).

Retaining structurally complex patches of forest anchored on large individual structures may support maintenance of desired conditions for martens and could be prioritized during forest management activities. Specifically, large diameter (>80 cm) snags and live trees with obvious cavities, signs of decay (e.g., heart rot fungi), or decay pathways (e.g., large scars, broken tops) can be readily identifiable and could serve as anchor points for retention. To maximize the value of retained forest, the area surrounding anchor points would include features such as a relatively high number of larger diameter logs, relatively high canopy cover, a diversity of tree sizes, and additional large diameter snags and trees (Figure 4). Although our scope of inference is generally limited to the scale of our sampling, our results are consistent with conditions preferred by martens (e.g., heterogeneity, structural complexity) across broader scales. Accordingly, we suggest that the size of our sampled plots (i.e., 0.1–0.2 ha) could be considered a minimum recommended area for retention but that retaining larger areas would be of greater value when possible.

These represent achievable actions at a practical scale that could be applied to sustain wildlife habitat during forest management. Large individual trees and snags create structural and functional diversity and are considered

keystone attributes of forests worldwide, providing important nesting, breeding, roosting, and denning locations for a diversity of taxa (Tews et al. 2004). Examples of wildlife in our study systems that use large trees and snags include, but are not limited to bats, birds (e.g., raptors, swallows, woodpeckers), small mammals (e.g., flying squirrels, voles), and larger mammals (e.g., bears; Hunter and Bond 2001, Mazurek and Zielinski 2004). Other species in our study systems, such as spotted owls (*Strix occidentalis*) and fishers (*Pekania pennanti*) appear to require large-diameter individual structures (e.g., for nest or rest sites) while also being associated with forest structural complexity and heterogeneity at fine spatial scales (Hunter et al. 1995, Zielinski et al. 2004, Purcell et al. 2009, North et al. 2017, Green et al. 2019, Zulla et al. 2022), similar to our findings for martens. Our recommendations therefore have the potential to benefit the broader wildlife community, which should be a principal consideration when developing management strategies (Zipkin et al. 2010).

CONSERVATION IMPLICATIONS

Supporting species persistence presents a substantial challenge to conservation in a rapidly changing world. A fundamentally important component of species conservation for martens and other forest-dependent wildlife involves sustaining suitable forest conditions into the future, which will increasingly require clear guidance and purposeful actions. Our results suggest that targeted retention of large and decadent trees situated within structurally complex patches of forest could benefit marten populations during forest management and thereby facilitate achievement of conservation objectives.

ACKNOWLEDGMENTS

This publication represents the views of the authors, and any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the United States Government. We thank C. L. Gress, J. L. Hutchinson, P. N. Manley, E. L. McGregor, K. M. Slauson, M. M. Williams, and W. J. Zielinski for critical administrative and technical support. The Yurok Tribe was instrumental in allowing access to tribal lands and we acknowledge tribal employees including K. W. Barnes, T. R. Hayden, and C. J. West for their efforts. Many field technicians assisted with data collection including R. Adamczyk, L. Bailey, B. Barry, T. Bentz, T. Charbonnier, M. Dao, M. Cokeley, E. Duprey, J. Easter, M. Faber, C. Garcia, T. Gettleman, T. Gosney, C. Heard, I. Holl, S. Hubert, L. Kreiensieck, M. Linnell, L. Manden, K. Mansfield, M. Marquez, L. McCoy, C. McNamara, A. Morris, E. Paton, K. Phillips, P. Tweedy, J. Vance, C. Wood, and H. Ziemer. Project funding was provided by United States Department of Agriculture Forest Service–Lassen National Forest and the United States Fish and Wildlife Service. Green Diamond Resource Company, National Council for Air and Stream Improvement, Oregon State University, and United States Department of Agriculture Forest Service–Pacific Southwest Research Station provided logistical assistance. Research was further supported by an appointment to the United States Department of Agriculture Forest Service Research Participation Program, administered by the Oak Ridge Institute for Science and Education, through an interagency agreement between the United States Department of Energy and the United States Department of Agriculture.

CONFLICTS OF INTEREST STATEMENT

The authors declare that there are no conflicts of interest.

ETHICS STATEMENT

Capture procedures were approved by the Institutional Animal Care and Use Committee at Oregon State University (permits 3944 and 4367) and were permitted by the California Department of Fish and Wildlife (permits 4683, 803099-01). Capture and immobilization techniques followed guidelines for the use of wild mammals in research established by the American Society of Mammalogists (Sikes et al. 2016).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Matthew S. Delheimer  <http://orcid.org/0000-0001-7310-0190>

Katie M. Moriarty  <http://orcid.org/0000-0002-3348-3403>

Holly L. Munro  <http://orcid.org/0000-0001-6026-5607>

Keith A. Hamm  <http://orcid.org/0000-0002-3660-3255>

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Associate Editor: Masumi Hisano.

How to cite this article: Delheimer, M. S., K. M. Moriarty, H. L. Munro, D. A. Early, K. A. Hamm, and R. E. Green. 2023. Structural complexity characterizes fine-scale forest conditions used by Pacific martens. *Journal of Wildlife Management* 87:e22388. <https://doi.org/10.1002/jwmg.22388>