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Cover of tall trees best predicts California spotted owl habitat

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ABSTRACT

Restoration of western dry forests in the USA often focuses on reducing fuel loads. In the range of the spotted owl, these treatments may reduce canopy cover and tree density, which could reduce preferred habitat conditions for the owl and other sensitive species. In particular, high canopy cover (≥70%) has been widely reported to be an important feature of spotted owl habitat, but averages of stand-level forest cover do not provide important information on foliage height and gap structure. To provide better quantification of canopy structure, we used airborne LiDAR imagery to identify canopy cover in different height strata and the size and frequency of gaps that were associated with owl nest sites, protected activity centers (PACs), and territories within four study areas and 316 owl territories. Although total canopy cover was high in nest stands and PAC areas, the cover in tall (> 48 m) trees was the canopy structure most highly selected for, while cover in lower strata (2–16 m) was avoided compared to availability in the surrounding landscape. Tall tree cover gradually decreased and lower strata cover increased as distance increased from the nest. Large (> 1000 m^2) gaps were not found near nests, but otherwise there was no difference in gap frequencies and sizes between PACs and territories and the surrounding landscape. Using cluster analysis we classified canopy conditions into 5 structural classes and 4 levels of canopy cover to assess the relationship between total canopy cover and tree size within nest sites, PACs, and territories. High canopy cover (≥70%) mostly occurs when large tree cover is high, indicating the two variables are often confounded. Our results suggest that the cover of tall trees may be a better predictor of owl habitat than total canopy cover because the latter can include cover in the 2–16 m strata – conditions that owls actually avoid. Management strategies designed to preserve and facilitate the growth of tall trees while reducing the cover and density of understory trees may improve forest resilience to drought and wildfire while also maintaining or promoting the characteristics of owl habitat.

1. Introduction

Historically dry western forests, on average, had lower tree densities, canopy cover and fuel loads than forests today largely due to the absence of frequent, low-severity fire for much of the 20th century (Knapp et al., 2013; Collins et al., 2015; Stephens et al., 2015; North et al., 2016). To increase resistance and resilience to current high-intensity wildfire and increasingly frequent and severe drought conditions (Graumlich, 1993; Asner et al., 2016; Margulis et al., 2016), managers often use mechanical thinning and managed fire to create

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some semblance of these historic stand conditions (Agee et al., 2000; Agee and Skinner, 2005; North et al., 2009). Such treated forests, however, often lack some of the structural features that have been linked with old-growth associated species such as the spotted owl (*Strix occidentalis*), fisher (*Martes pennanti*) and northern goshawk (*Accipiter gentillis*) (McClaren et al., 2002; Lee and Irwin, 2005; Purcell et al., 2009; North et al., 2010; Truex and Zielinski, 2013; Tempel et al., 2014; Sweitzer et al., 2016). In particular, throughout much of the western U.S., managing for the high canopy cover and tree density conditions of preferred spotted owl habitat may conflict with reducing ladder and canopy bulk density fuels, and stem density to improve a forest's fire and drought resilience (Zabel et al., 1995; North et al., 1999; Stephens et al., 2014; Jones et al., 2016; Stephens et al., 2016). The uncertainty about the effect of forest treatments on owls has often led to forest plans that separate landscapes into distinct restoration (i.e., managed to reduce fuels and stand density) and owl habitat zones (managed to preserve and increase high canopy cover) (Ager et al., 2007; Carroll and Johnson, 2008).

High (≥70%) levels of canopy cover within both owl territories and their core use areas (120 ha management designated Protected Activity Centers [PACs]) have been associated with greater owl occupancy and survival (Tempel et al., 2014; Tempel et al., 2015), and higher reproduction at nest sites (North et al., 2000). High canopy cover is commonly used to identify potential habitat areas and determine management options. Yet, canopy cover can be a difficult management target because estimates significantly vary depending on how many measurements are taken, the observer's viewing angle (i.e., closure vs. cover sensu Jennings et al., (1999)) and whether estimates are derived from direct field measurements (ex. spherical densiometer, densitometer, or 'moosehorn'), indirect interpretation (i.e., using aerial photographs or Landsat imagery) or modeled from non-spatial plot data (i.e., such as the Forest Service's estimates using the Forest Vegetation Simulator) (Fiala et al., 2006; Korhonen et al., 2006; Christopher and Goodburn, 2008; Paletto and Tosi, 2009). Field plots are used to record tree size and foliage characteristics, but sample size is often small, which makes it difficult to extrapolate across the large, diverse forest conditions used by owls.

Canopy cover estimates using Landsat imagery or interpreted aerial photographs can sample larger areas, but neither method can be used to identify the tree size or height of foliage cover, and must be categorized (e.g., 0–39%, 40–69% and ≥70%) to meet the wide variety of ages and structures of forests (Tempel et al., 2016). Given the challenges of measuring canopy cover, both managers and researchers have often resorted to coarse classifications such as the widely used California Wildlife Habitat Relationships (CWHR) classes (Tempel et al., 2014) that are known to simplify and only roughly correlate with patterns of actual animal use (Purcell et al., 1992; Block et al., 1994; Howell and Barrett, 1998). Regardless of how it is estimated as a stand-level characteristic, canopy cover does not provide information on the height and distribution of foliage or the size and frequency of forest gaps (Jennings et al., 1999). Consequently, it is unclear how foliage and gaps are either distributed within owl use areas, or how best to assess and then establish management objectives for sustaining and enhancing owl habitat.

In this study we use airborne LiDAR data to measure canopy structure both intensively and accurately within all owl territories (n = 316 territories within a cumulative 420,478 ha) found in four large study areas having a variety of management histories in the central and southern Sierra Nevada. Three of these locations are long-term owl demographic study areas, and include an area in Sequoia/Kings Canyon National Park (SEKI) where the only logging occurred 75–120 years ago in localized, limited areas. SEKI includes forests with restored fire regimes, and has the only known non-declining population of spotted owls that have been studied in California. The fourth site, Tahoe National Forest, while not a demographic study area, did survey owl occupancy and reproduction over an extensive area for which LiDAR data was collected. The LiDAR data allowed us to map forests in high fidelity, measuring total canopy cover, the distribution of cover by height strata, and opening sizes and frequencies. We analyzed habitat at three scales for each owl pair: nesting area (~4 ha), the surrounding Protected Activity Center (~120 ha), and the encompassing territory (~400 ha). Using the data on tree cover in different height strata and how they are associated, we used cluster analysis to identify common forest structural conditions. We then compared structural conditions between owl use areas and the surrounding forest with a complete LiDAR sampling of the landscape within a 5 km radius.

The goal of this study was to use our large sample size and high fidelity measurements over large areas to examine which attributes of forest structure are most strongly associated with California spotted owl habitat. Using LiDAR measures of forest structure, we examined the following specific questions:

- Which canopy structures are most strongly associated with different scales of owl habitat use, focusing on the nest, PAC and territory?
- How does the percentage of overstory tree canopy area in different height strata and gap sizes compare between owl use areas and across study areas?
- How strongly selected are different canopy attributes at nests compared to the available landscape and how does that change with distance from the nest?
- How are structure classes distributed between different owl use areas and what is the relationship between these structure classes and total canopy cover?

2. Methods

2.1. Study areas

The four study areas are located on the western slopes of California's Sierra Nevada Mountains in predominantly ponderosa pine (*Pinus ponderosa*) and mixed-conifer forests, and extend over a range of 3^0 latitude or about 320 km (Fig. 1). The Tahoe study area (311,930 ha) encompasses most of the Tahoe National Forest and is dominated by ponderosa pine, incense cedar (*Calocedrus decurrens*) and black oak (*Quercus kelloggii*) on drier, lower elevation locations, and a combination of ponderosa and sugar pine (*P. lambertiana)*, incense cedar, Douglas-fir (*Pseudotsuga menziesii*) and white and red fir (*Abies concolor* and *A. magnifica)* generally above 1300 m in more mesic conditions. At higher elevations (generally > 2000 m) and in the eastern-most portion of the owl use area, red and white fir and Jeffrey pine (*P. Jeffreyi*) dominate forest composition. Areas of the Tahoe NF are checkerboarded with private ownership and much of the forest has been heavily selectively logged over the last century, resulting in scattered large individual trees and small pockets of old growth (Taylor, 2004). Since about the 1930s almost all fires have been suppressed leaving forests often in a fuel-loaded condition with high stem density and canopy cover.

The Eldorado Study Area (40,549 ha) includes an owl demographic study area on the Eldorado National Forest (Tempel et al., 2016). It is located east of Georgetown on steep terrain surrounding the Rubicon and middle Fork of the American rivers between 300 and 2500 m elevation. It is primarily mixed conifer with occasional black and canyon live oaks (*Quercus chrysolepis*), tanoak (*Notholithocarpus densiflorus)* and bigleaf maple (*Acer macrophyllum*). At higher elevations some of the study area includes red fir and lodgepole pine (*Pinus contorta*). The Eldorado National Forest was logged selectively, often removing the largest trees, and fire suppressed through much of the last century (Darr, 1990). Portions of the demographic study area have a checkerboard of private land ownership, much of which is owned by SIMORG Forests LLC. About 50% of the owl study area burned, much of it at high severity, in the 2014 King Fire (Jones et al., 2016). The LiDAR data we use is from an acquisition completed before 2014.

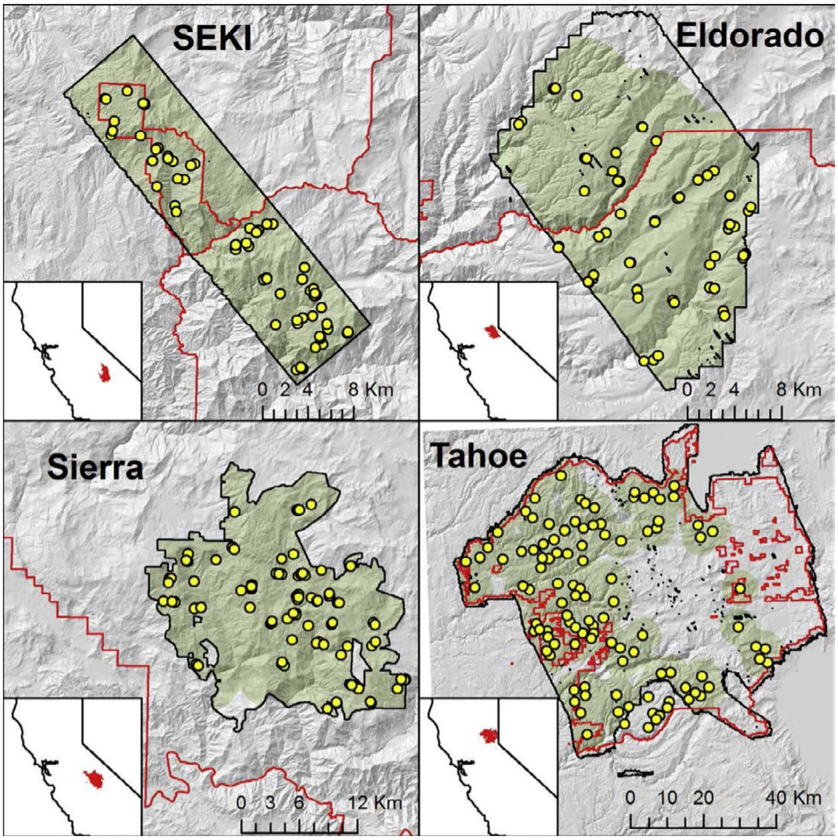

Fig. 1. The location in California (inset) of each of the four study areas. The black line shows the area of the LiDAR acquisition, circles indicate owl nest sites and green shading indicates the study area analyzed (i.e., within a 5 km radius of the PAC nests centroid). The background grey shading indicates the topography of the area. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The Sierra Study Area (41,080 ha) is on the Sierra National Forest, east of Fresno between 300 and 2900 m elevation. Both the Sierra study area and the nearby Sequoia-Kings Canyon study area (SEKI) are drier than the Tahoe and Eldorado areas (North et al., 2016). The Sierra study area is dominated by mixed-conifer forests, but on lower and drier sites includes ponderosa pine, interior live (*Quercus wislizeni*) and canyon oaks. Higher elevations include red fir, lodgepole pine and western white pine (*Pinus monticola*) (North et al., 2002). Most wildfire has been suppressed on the Sierra National Forest for decades but the forest was not as extensively logged as the more northern study areas (North et al., 2005). Many large, old trees remain in stands that were selectively logged and areas of old growth remain on steeper slopes because topography limited access for mechanical logging (North et al., 2015).

The Sequoia/King Canyon (SEKI) area (26,919 ha) is located on the western side of the two national parks of the same name and is mostly comprised of ponderosa pine and mixed-conifer forest types between 425 and 3050 m in elevation. Within the mixed-conifer zone there are several giant sequoia (*Sequoiadendron giganteum*) groves. With the exception of localized hazard tree removal and small areas of late 19th century logging (Stohlgren, 1992), these forests have not been logged (Vankat and Major, 1978). In addition, although many fires were suppressed in the first half of the 20th century, fire has been restored throughout much of the study area beginning in the 1970s (Parsons et al., 1986). Of California's four demographic study areas, SEKI is the only owl population that has been stable to expanding (Franklin et al., 2004; Blakesley et al., 2010; Conner et al., 2013; Tempel et al., 2014; Tempel et al., 2016). Therefore in our analyses we often compare SEKI forest structure to the three other study areas because it may provide more favorable habitat relative to the more heavily logged and fire-suppressed areas on the national forests.

2.2. Spotted owl data

The three study areas (Eldorado, Sierra, and SEKI) that encompass California spotted owl demographic studies had similar survey methods (Blakesley et al., 2010), whereas slightly different owl survey methods were used in the Tahoe study area. For the three demographic areas, owls were annually surveyed from at least 1993 to the present (Tempel et al., 2016). All three areas contained a core zone that was completely surveyed (i.e., known territories as well as areas not containing owls). Some individual owl territories were added over time that surrounded core areas to increase sample size for demographic analysis, while a portion of SEKI was deleted in 2006 due to funding limitations. Surveys were conducted from April 1 to August 31 in the Eldorado study area and from March 1 to September 30 in the Sierra and SEKI study areas. SEKI was not surveyed in 2005 due to budget limitations that year. Spotted owl vocalizations were used as vocal lures and broadcast at designated survey stations or while walking survey routes. The sex of owls was initially determined by the pitch of territorial 4-note calls (Forsman et al., 1984). If owls were detected during nocturnal surveys, diurnal surveys were conducted as a follow up to band unmarked birds, re-sight marked birds, assess reproduction, locate nesting/roosting areas, and band fledglings (Franklin et al., 1996).

Owl surveys in the Tahoe National Forest were conducted for at least two years before and two years after in areas where management treatments (e.g., thinning to reduce fuel loads) were conducted. As such the Tahoe area did not have a core study area that was continually sampled but instead had focal surveys that shifted with management activities. However, owl survey methods were similar to those used on the owl demographic study areas.

In each study area, our analysis focused on confirmed owl pair nest sites that were occupied for at least one year. To insure that the LiDAR assessed forest conditions relevant to owl use, we only used 2001–2013 owl nest sites. We conducted our analysis at four different scales related to owl use and management. The nest site was considered a four-hectare area immediately surrounding each nest tree or snag. The size of the area around a nest that may influence owl selection has not been assessed but several studies have suggested canopy cover and microclimate conditions may be factors in nest site selection (LaHaye et al., 1997; LaHaye and Gutierrez, 1999; North et al., 2000). We used four hectares as a conservative estimate for the area over which forest structure might influence microclimate (Ma et al., 2010). The protected activity center (120 ha or 300 ac) has been a forest management construct designed to approximate a core area that receives heavy use (Verner et al., 1992). In practice, agencies define these areas as a polygon of the best available habitat (often related to tree size and disturbance history) around a nest location (Verner et al., 1992; Tempel and Gutierrez, 2013) that often approximates a circle. Without knowing the exact shape of each PAC, for our analysis we defined this area as a circle of 120 ha (300 ac) immediately around the centroid of all nests belonging to an individual owl (Berigan et al., 2012). To estimate forest characteristics within a territory, we used territory sizes within the three study areas that were delineated as 400 ha, 302 ha and 254 ha for the Eldorado, Sierra and SEKI studies, respectively (Tempel et al., 2016). We did not have similar information for the Tahoe study area. Thus we fitted a regression line of territory size against latitude using the three demographic studies areas, as well as a fourth demographic study area on the Lassen NF (639 ha), which resulted in an approximated territory size of 437 ha for the Tahoe study area.

To estimate availability in the surrounding landscape, we used a circle 5 km in radius from the calculated activity center of each territory. To evaluate how forest conditions may differ with potentially different owl uses (e.g., nesting vs foraging and the influence of a central place forager), we removed the PAC area from territory calculations. In contrast, we did not remove the nest areas from each PAC, because studies have shown that owls select multiple nest and roost locations throughout a PAC (LeHaye et al., 1997).

2.3. Analysis of canopy structure

LiDAR data was acquired over our study areas between 2010 and 2015 (Table 1). We used the digital terrain models prepared by the acquiring vendor or organization. We processed the LiDAR data using the USDA Forest Service's Fusion software package (version 3.60, http://forsys.cfr.washington.edu/fusion/fusionlatest.html) (McGaughey, 2016) to produce metrics describing the canopy structure. In the processing, we normalized all laser returns to height above the digital terrain models. There were no major disturbances such as large high severity fire on our study areas between the time of the collection of the owl field data and the acquisition of the LiDAR data.

We used several strategies to generate the widest possible range of canopy structure measurements. We used the FUSION gridmetrics utility to produce 30 m resolution rasters of statistical measures of the vertical distribution of LiDAR return heights. This provided measurements of percentile return heights (e.g., 95th percentile height is the height at which 95% of returns fall below), standard deviation of return heights, and skew and kurtosis of return heights. These quantify canopy structures that have been associated with owl use: tall tree height, the variability in tree heights and how evenly or skewed tree heights are, respectively. We calculated these statistical descriptors excluding returns < 2 m to exclude returns representing the ground, shrubs, and saplings. The gridmetrics utility also produced a measurement of canopy cover calculated as the count of returns above 2 m divided by the count of all returns.

Researchers are beginning to analyze forests as clumps of trees and openings (e.g., Larson and Churchill, 2012). We developed methods for this study to do this using the LiDAR data. Several studies have found that characteristic tree clump and opening patterns emerge at scales of 0.5–1 ha (Harrod et al., 1999; Larson and Churchill, 2012; Knapp et al., 2012; Lydersen et al., 2013). We therefore analyzed these patterns at a 90 m (0.81 ha) scale. We created a canopy surface model with a grid cell size of 0.75 m^{-2} and assigned the height above the digital terrain model of the highest return to each grid cell. We used the canopy surface model to identify tree approximate objects (TAOs) using the watershed segmentation algorithm implemented in the TREESEG utility in the FUSION package (Fig. 2). The TREESEG utility provided a raster map of the modeled canopy area of each TAO with the maximum height of each TAO assigned to the entire canopy area for that TAO (Fig. 3a). We then reclassified each TAO into the following height strata: 2–16 m, 16–32 m, 32–48 m, and > 48 m so that clumps of overstory trees with similar heights could be identified. Areas with no canopy > 2 m were considered openings. We measured the area in each strata using a moving 90 by 90 m window with measurements centered at 30 m spacing to match the raster cells of the statistical and canopy cover measurements (Fig. 3b). The use of an overlapping moving window had the practical effect of smoothing the measurements of tree clump and opening areas. We report metrics as the area in each stratum for each grid cell.

We also investigated whether the presence and density of larger gaps that might affect microclimate and protective cover conditions for the owls, as well as providing foraging opportunities for the owl, were negatively associated with owl habitat. We defined gaps following methods (Lydersen et al., 2013) that set a minimum size of 112 m^2, the approximate crown area of a dominant tree. We binned gaps larger than this minimum size into categories suggested by research on forests that have frequent fire regimes (Harrod et al., 1999; Larson and Churchill, 2012) and operational sizes often used by managers in thinning prescriptions (Knapp et al., 2012; North and Rojas, 2012; Stine and Conway, 2012). We reported the percentage of area and frequency for gaps in the categories 112–1000 m^2, 1000–5000 m^2, 5000–10,000 m^2, and > 10,000 m^2 (Fig. 3c).

2.4. Statistical analysis

To identify canopy variables most strongly associated with owl use, we initially used three statistical approaches to compare structures at nest sites against the surrounding landscape: niche overlap modeling, general linear models and random forest. All three approaches produced similar results and hereafter we base inference on niche overlap modeling because it provides a quantitative measurement of distinction

Table 1
Attributes of owl territories and LiDAR data used for the four study areas.

Owl data	Tahoe	Eldorado	Sierra	SEKI
No. of nests	64	58	63	131
Area (ha) of coverage within 5 km of a nest	311,930	40,549	41,080	26,919
Elevation range within 5 km of a nest	292–2673	711–2190	390–2961	835–2643
Year(s) data acquired	2013 & 2014	2012	2010 & 2012	2015
Acquirer	NCALM[a]	NCALM[a]	Watershed Sciences[b]	Carnegie Institution for Science
Instrument family	Optech	Optech	Leica	CAO[c]/Optech
# of returns/m[b]	10.3	8.1	12.3	14

[a] National Center for Airborne LiDAR Mapping.
[b] Now part of Quantum Spatial.
[c] Carnegie Airborne Observatory modification of Optech (see Asner et al., 2012).

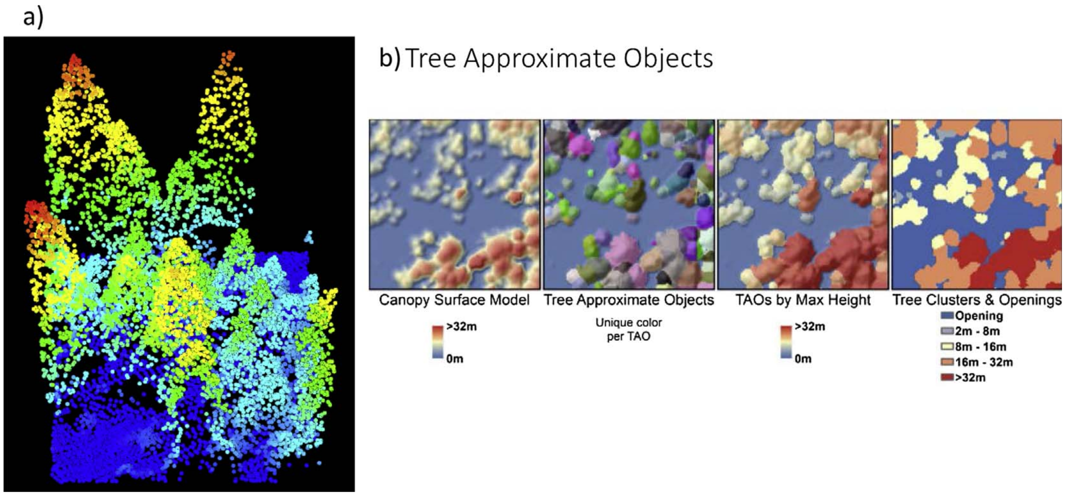

Fig. 2. Example of (a) a LiDAR point cloud where returns are color-coded by height; and (b) how tree approximate objects (TAOs) and gaps are derived from the point cloud data. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

between two distributions (Mouillot et al., 2005; Broennimann et al., 2012). Niche overlap compared the distribution of values of a structural variable across a landscape ('availability') relative to a specific location ('selection'). Smaller overlaps indicated that areas used by owls were more distinct from what was available across the landscape and by inference was selected by the owls (Fig. 4a).

Focusing on the canopy and gap attributes with the highest niche model ranks (Supplemental Table 1), we calculated the median, and standard deviation of each attribute as four different scales; nest sites, PACs, territories and the surrounding landscape within each study area. We then tested for significant differences between study areas using Student's post hoc ANOVA.

Spotted owls are central place foragers (Carey and Peeler, 1995), suggesting that canopy structure may change with distance from core locations (i.e., nesting and roosting sites). To evaluate changes in canopy conditions with distance from the nest, we assessed the niche decay function using annuli that expanded by 30 m per step. For highly ranked niche model variables, we plotted the percentage of niche overlap as a function of distance from owl nests for each of the four study areas.

Forests are often a complex assemblage of foliage in different strata. To quantify and describe how multiple canopy structures may commonly occur together, we created structure classes combining three core attributes of forest structure: tree height distribution, total canopy cover, and cover in different strata. These variables were analyzed using hierarchical clustering with the Ward method and the hclust

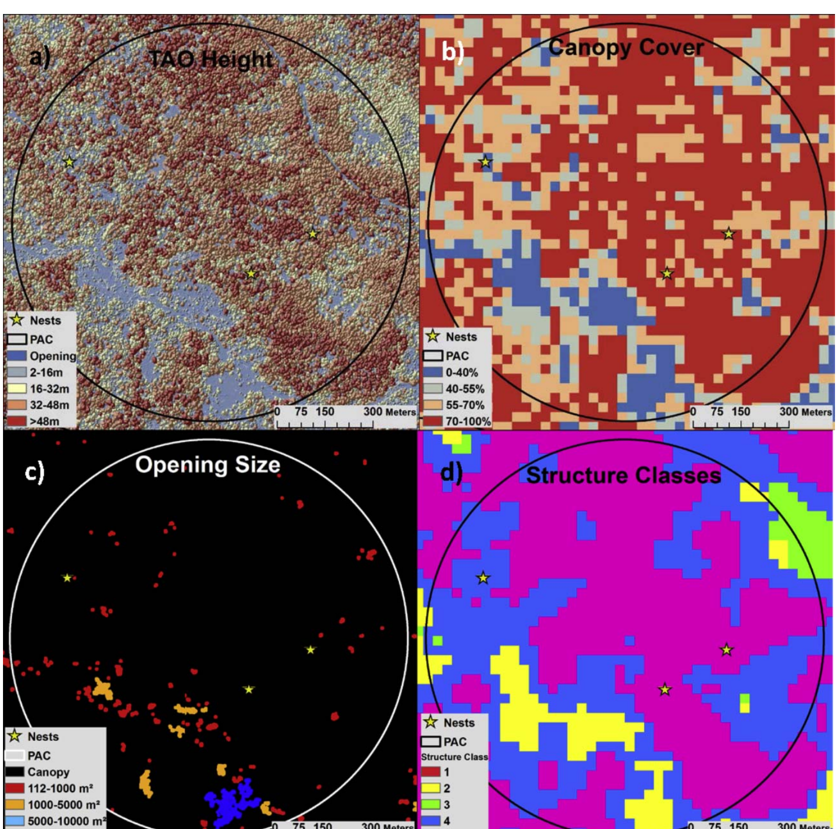

Fig. 3. Example of the distribution of (a) TAOs by height class; (b) total canopy cover; (c) opening size; and (d) structure class for the same PAC area (black circle) in the Eldorado study area. Stars indicate nest locations.

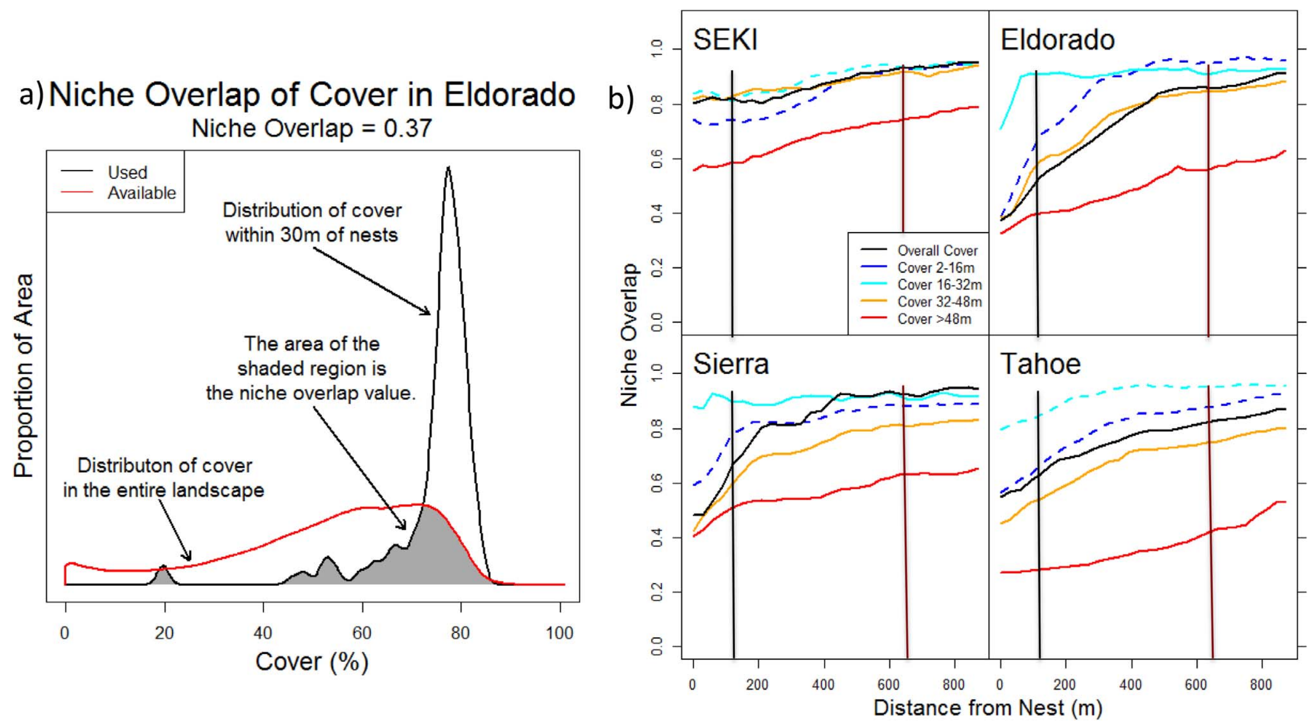

Fig. 4. (a) An annotated example of how niche overlap is calculated; and (b) graphs of niche overlap for total canopy cover and cover in four different height strata in each of the four study areas with distance (m) from the owl nest. Dashed lines are canopy structures that have lower values near the nest than in the surrounding landscape. Vertical lines indicate the distance defining the nest (black) and PAC (brown) areas.

function of the R statistical package (Team, 2013). Using dendrograms derived from 30,000 samples and structural characteristics of trial classes, we parsed conditions into five canopy structure classes that was the most parsimonious grouping that retained most (> 70%) of the original information (McCune and Mefford, 1999) (Supplemental Fig. 1). Within each of the five structure classes, we divided samples into four different canopy cover classes that previous research has suggested may be important thresholds to spotted owls; 0–39%, 40–54%, 55–69% and ≥70% canopy cover (Tempel et al., 2015, 2016). Therefore, we derived the percent area of each combination of canopy structure and canopy cover classes for nest, PAC, territory, and landscape areas.

3. Results

3.1. Canopy attributes associated with owl use

To determine which forest conditions were most distinct in areas used by owls versus the surrounding landscape, we evaluated 75 canopy structural attributes (Supplemental Table 1). The area of TAO canopy > 48 m was the most distinct metric for all study areas. The strongest nest and PAC selection for tall tree cover was in the Eldorado and Tahoe study areas presumably because both National Forests have been extensively logged and large, tall trees are rarer (Table 2). Area of TAO canopy 32–48 m, canopy cover, and measures of canopy height from LiDAR returns were moderately distinct from the surrounding landscape. Total area in gaps and gaps in different size ranges were among the least distinct. However, in the Tahoe study area, there were fewer small gaps (112–1000 m^2) within PACs compared to the surrounding landscape (Table 2).

Across all four study areas, median values for total canopy cover and cover in trees > 48 m were highest at nest sites, and consistently decreased as area expanded to PACs, territories and then the surrounding landscape (Table 3). We also found a similar trend of decreasing values from nest sites to landscape for the 32–48 m strata on the three National Forest study areas but not at SEKI. We found a reverse trend for cover in the 2–16 height strata with the lowest cover values near nest sites and increasing through larger scales. We did not find a consistent trend with changes in scale for cover values for the 16–32 m strata.

Across the entire study area, 20–40% of LiDAR returns were penetrating below 2 m indicating substantial area in openings. However, few of these openings were aggregated enough to reach the 112 m^2 threshold we used to define a 'functional' gap (an opening approximately equal to the canopy space occupied by a dominant tree). Gaps 112–1000 m^2 were rare within nest areas, and only accounted for 0.17–1.45% of the area in PACs and territories. Larger gaps were not found in nest areas. The area in gaps of 1000–5000 m^2 within PACs and territories ranged from 0.05 to 1.21% and we only found gaps > 5000 m^2 in the Sierra and Tahoe study areas (Table 3).

We found differences in canopy and gap conditions among the four study areas (Table 3). SEKI had lower canopy cover at nest sites, higher cover of tall trees (> 48 m) within nest sites, PACs and territories, and higher cover in the 32–48 m strata in territories. The Eldorado had greater cover than other areas in the 2–16 m cover in PACs and territories. The Sierra had lower total canopy cover in PACs and territories, and more gaps of all sizes, particularly those > 1 ha, in PACs and territories. The Tahoe had no distinguishing canopy cover conditions but did have high cover in gaps of all sizes at the territory scale (Table 3).

3.2. Changes in canopy structure with habitat scale

We examined spatially-explicit relationships by evaluating how niche overlap values changed with distance from the owl nest using a moving window and comparing each canopy attribute to its abundance in the surrounding (5 km) landscape (Fig. 4b). For all four study areas, the cover in tall (> 48 m) trees was the most distinct canopy attribute (i.e., the least niche overlap) starting at the nest site (the y intercept) and remained the most distinct over the 1000 m distance evaluated. The slope of the line for the cover of trees > 48 m continued to rise over 1000 m from the nest, suggesting that selection for tall trees may continue beyond the bounds of the PAC (618 m radius). Total canopy

Table 2
Niche values for different canopy structure attributes in four study areas and their overall mean comparing PAC and landscape habitat conditions. Bold values have low niche overlap (≤0.6) suggesting a structure selected for within PACs compared to the landscape. Metrics in italics are negative (i.e., have lower values in PACs compared to landscape). Metric type indicates the data used to calculate the structure value and pixel size indicates the dimension of the pixel used in the calculation. Canopy cover was calculated as the proportion of LiDAR returns greater than 2 m in height above the ground divided by all returns. Gap area was calculated as the area of the 0.75–2 m canopy surface model with no returns > 2 m.

Metric	Eldorado	SEKI	Sierra	Tahoe	Mean	Metric type/Pixel size
Canopy area TAO's > 48 m	**0.49**	0.66	**0.6**	**0.37**	**0.53**	TAO/90 m
Canopy area TAO's > 32–48 m	0.75	0.87	0.75	0.71	0.77	TAO/90 m
95th percentile lidar return height	0.81	0.75	0.79	0.76	0.78	Returns/30 m
75th percentile lidar return height	0.81	0.75	0.8	0.76	0.78	Returns/30 m
50th percentile lidar return height	0.81	0.75	0.81	0.77	0.78	Returns/30 m
Std Dev. of lidar return heights	0.83	0.79	0.8	0.77	0.8	Returns/30 m
25th percentile lidar return height	0.81	0.76	0.83	0.79	0.8	Returns/30 m
Canopy area TAO's 2–16 m	0.8	0.76	0.84	0.82	0.81	TAO/90 m
Canopy cover from lidar returns	0.75	0.88	0.87	0.78	0.82	Cover/30 m
Total gap area	0.75	0.89	0.88	0.77	0.82	TAO/90 m
Area in gaps 112–1000 m^2	0.91	0.91	0.94	**0.56**	0.83	Gap/90 m
Area in gaps 5000–10,000 m^2	0.9	0.77	0.88	0.88	0.86	Gap/90 m
Area in gaps > 10,000 m^2	0.81	0.88	0.86	0.89	0.86	Gap/90 m
Area in gaps 1000–5000 m^2	0.96	0.89	0.86	0.85	0.89	Gap/90 m
Canopy area TAO's 16-32 m	0.93	0.81	0.91	0.94	0.9	TAO/90 m

Table 3
Median percent cover of total canopy cover, cover by height strata and cover of different gaps by size class in owl nests, PACs, territories and the surrounding landscape in four study areas. Comparing values within the same scale (ex. all nests), **bold** values are significantly higher and ***italic bold*** values significantly lower than the values in the other three study areas ($p < 0.05$, post hoc ANOVA). Landscape values are medians calculated from the whole landscape area and as single values are not included in the ANOVA analysis.

		Total and by Stratum Canopy Cover (%)					Cover (%) in Gaps by Size Class			
Area	Scale	Total CC	> 48 m	32–48 m	16–32 m	2–16 m	112–1000 m^2	1000–5000 m^2	5000–10,000 m^2	> 10,000 m^2
SEKI	Nest	***67.9***	**23.7**	26.6	19.4	6.7	0.02	0	0	0
	PAC	66.8	**20.6**	29.3	***20.8***	9.3	0.46	0.2	0	0
	Terr	63.9	**16.6**	**30.5**	23.3	11.6	0.59	0.31	0	0
	Land	65.9	3.2	24.1	26.4	11.7	0.82	0.54	0.18	0.42
Eldo.	Nest	76	14.7	38.1	31.8	5.1	*0*	0	0	0
	PAC	67.6	8.3	25.6	35.8	**16.9**[b]	0.17	0.05	0	0
	Terr	61.8	4.8	20.8	36.7	**25.7**[b]	0.39	0.26	0	0
	Land	55.8	0	9.9	32.4	22.2	0.73	0.57	0.22	1.7
Sierra	Nest	75.9	9.4	30.4	24.2	6.2	0.20	**0**[a]	0	0
	PAC	***59.6***	9.2	27.4	24.8	7.7	0.88	**1.03**	0	**0.60**
	Terr	***52.3***	5.5	22.6	25.2	9.1	1.45	1.21	0.3	1.57
	Land	55.7	0	14.9	22.8	9.4	1.51	1.28	0.55	4.18
Tahoe	Nest	73.7	12.5	41.5	25.6	3.6	0.01	0	0	0
	PAC	67.2	6.9	31.6	32.7	9.9	0.72	0.51	0	0
	Terr	62.2	4.3	22.6	35.4	12.1	1.16	0.81	0.21	0.71
	Land	46.2	0	2.4	26.9	10.1	1.93	1.43	0.51	4.07

[a] Although all the cover values for gaps 1000–5000 m^2 at nest locations are zero due to rounding, the Sierra value is significantly higher than the values at the other three study areas.
[b] The high percentage of cover in the 2–16 m stratum on the Eldorado is influenced by a checkerboard of private ownership lands, many of which contain young plantations in this height class.

cover continued to rise across the 1000 m measured, but had the lowest niche overlap values between 0 to approximately 500 m on the Eldorado, Sierra and Tahoe study areas. In contrast, canopy cover at SEKI was not a selected canopy attribute except right at the nest site (Table 3).

3.3. Structure classes and canopy cover

Using the percent cover of TAOs in different height strata within over 30,000 pixels (each 30 by 30 m), hierarchical cluster analysis produced a dendrogram that had five structure classes retaining > 70% of the information (McCune and Mefford, 1999) (Supplemental Fig. 1). Understory (class 1) is dominated by tree cover in the 2–16 m strata, Openings (class 2) has low total canopy cover and more large gaps, Ladders (class 3) by cover in the 16–32 m strata, Co-dominants (class 4) by cover in the 32–48 m strata and Tall Trees (class 5) by cover in the > 48 m strata (Fig. 5).

Taking each of the classes and subdividing them into four canopy cover classes (0–39%, 40–54%, 55–69% and ≥70%), we examined how the percentage of total area of each structure/canopy cover class changed between nest sites, PACs, territories, and landscapes in each of the four areas (Fig. 6). Canopy cover conditions ≥70% (right slant hatching in Fig. 6) was dominated by the Tall Tree structure class (purple bars in Fig. 6) indicating that tall trees and high canopy cover co-vary. The Co-dominant structure class was dominated by canopy cover categories ≥55%, as the Understory and Ladders structure classes had fairly equal canopy cover distributions, while the Openings structure was dominated by 0–40% canopy cover. Nest sites and PAC areas were dominated by the Tall Tree and Co-dominant structure classes with high canopy cover (i.e., > 55%), but territories and landscapes had a much more even distribution of structure classes suggesting greater heterogeneity of forest conditions at these larger scales. Trees > 32 m, and especially > 48 m, were almost always associated with high canopy cover in large part because the large canopy area of these trees created high canopy cover. Locations with high canopy cover but without tall trees were not associated with owl nest sites or PACs.

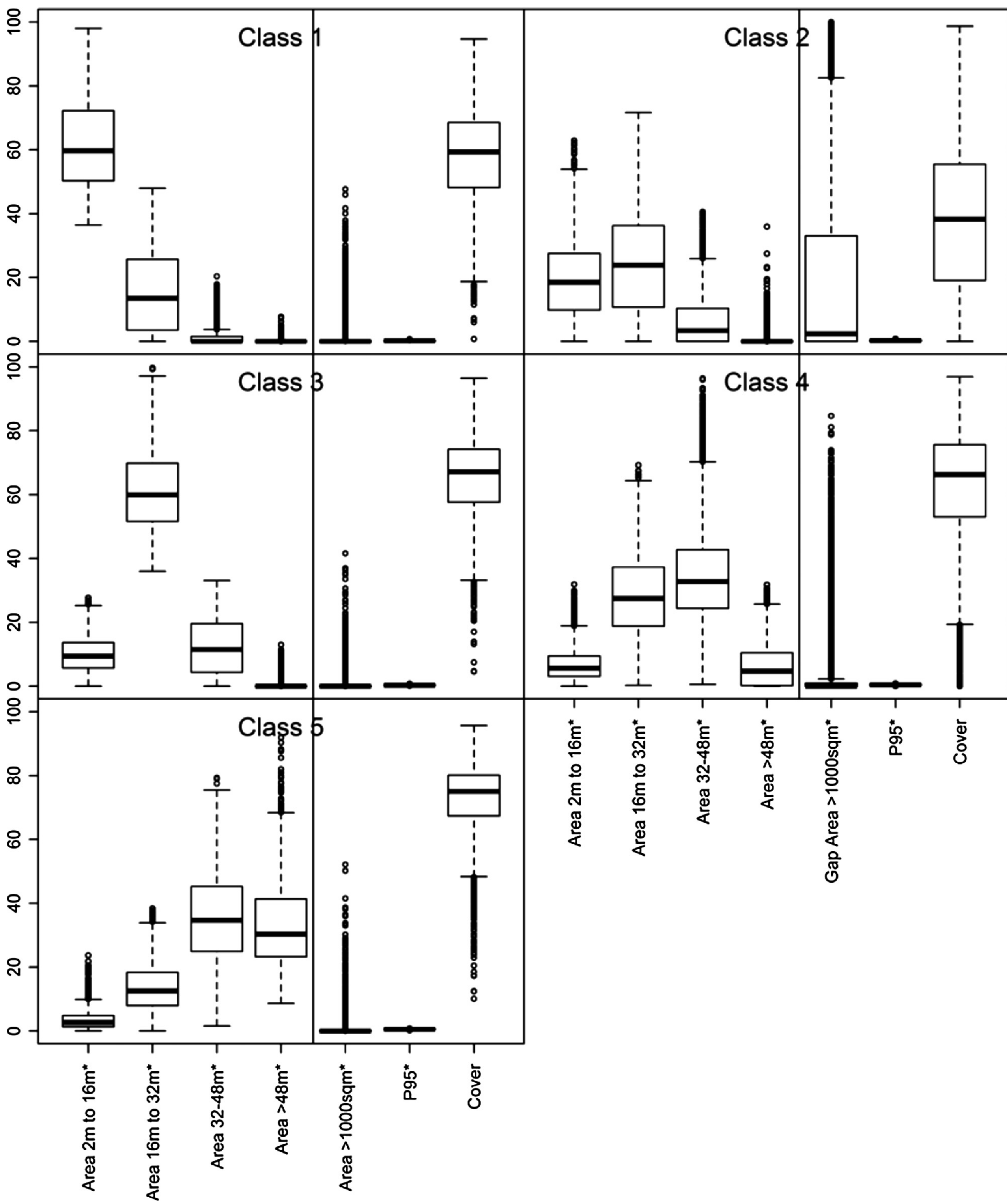

Fig. 5. Boxplots of canopy attribute values for each of the five identified structure classes. The boxplot contains the 25–75% range of values and the interior line is the median value. Whiskers show the range from 10 to 90% and dots are outliers. Gap area > 10,000 m^2, P95 (maximum height recorded from 95% of returns) and canopy cover are shown for reference but were not used in the cluster analysis to determine the structure classes.

4. Discussion

We found that the height of canopy cover matters, and the retention and promotion of large trees and the cover they provide may more directly benefit owl habitat than high levels of total cover from any canopy strata. Median values of total canopy cover were higher in nest and PAC areas than territories and the surrounding landscape, but the most distinct niche selection was cover of trees > 48 m. Tall tree cover is rarer on national forest lands (Table 3), and yet what is available is consistently found in nest and PAC areas. Our structure class analysis indicated that > 70% total canopy cover rarely occurred except when cover of Tall Trees and Co-dominants was high (classes 4 and 5 in Fig. 6), suggesting these two variables were often confounded. This covariance may explain why canopy cover, which is easier to measure

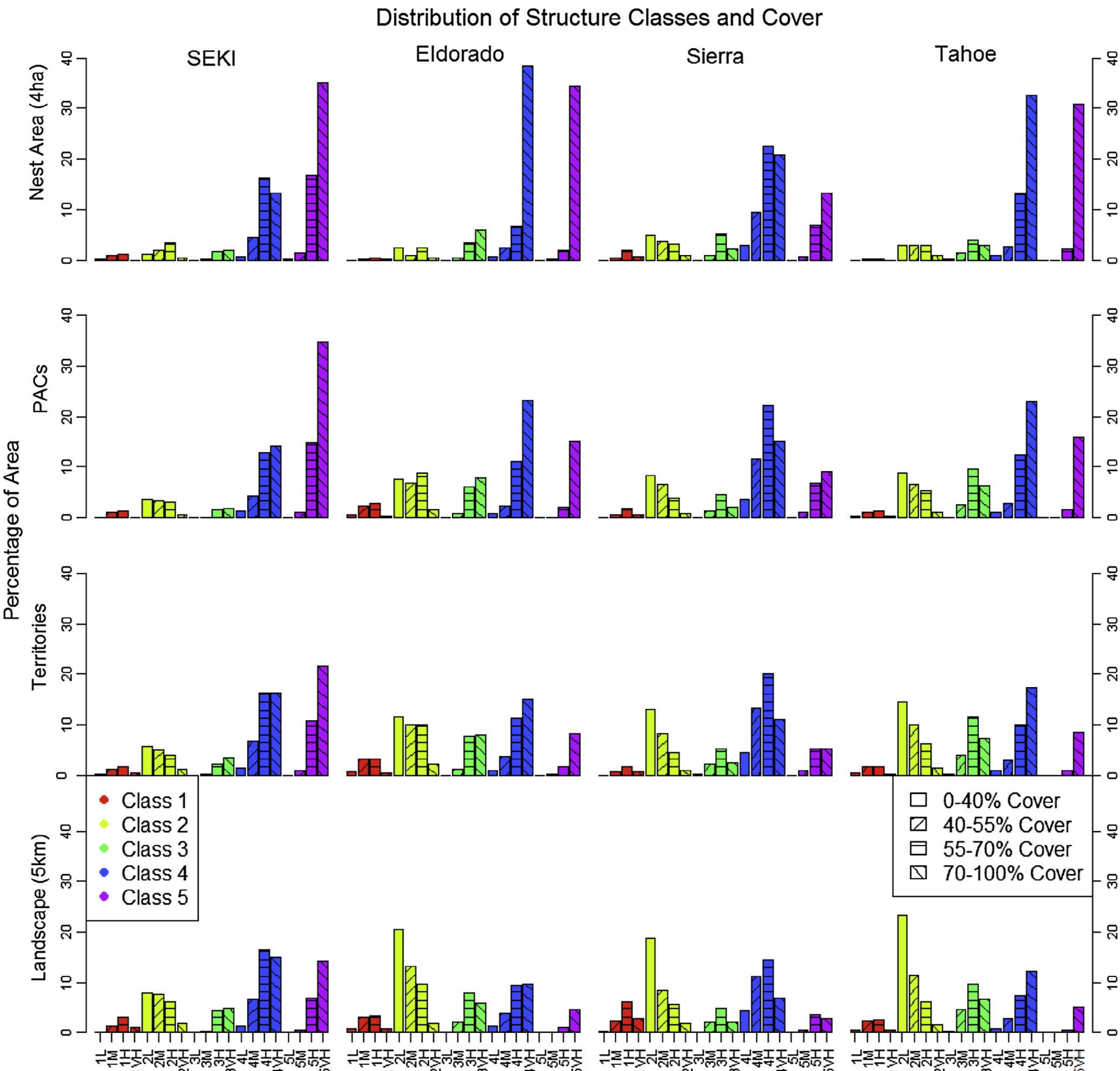

Fig. 6. Frequency distribution (% of total area) for each of the structure classes by nest, PAC, territory and surrounding landscape for each of the study areas.

and often recorded, has been reported as the forest condition associated with spotted owls rather than the cover in tall trees. Furthermore, although cover in the 2–16 strata can contribute to total canopy cover values, our analysis indicates nest sites and PACs actually have less cover in this stratum than is present in territories and the surrounding landscape, suggesting owls avoid this condition.

4.1. Large trees and canopy cover

Spotted owl research has consistently shown that owls are associated with large trees and total canopy cover (Call et al., 1992; Verner et al., 1992; North et al., 2000; Tempel et al., 2014; Tempel et al., 2016), but research has rarely parsed canopy structure into different height strata or assessed gap conditions. Our results confirm some widely reported owl habitat characteristics (Hunsaker et al., 2002; Blakesley et al., 2005; Seamans and Gutierrez, 2007), using larger sample sizes and a more quantitative measure of canopy structure than previous ground-based plot sampling and aerial photograph interpretation (although see Garcia-Feced et al., (2011)). Owl nest sites are in areas of high canopy cover that are dominated by a high percentage of cover in tall trees and few canopy gaps. Several studies of California spotted owl nest stands have also reported a selection for areas with high levels of canopy cover and groups of large (> 75 cm dbh) trees (LaHaye et al., 1997; Blakesley et al., 2005).

The high canopy cover levels associated with spotted owl use areas has suggested that gaps were generally avoided or might reduce habitat quality. We found that gaps of any size, even as small as those in our 112–1000 m^2 category were rare in nest sites. Few studies have measured or discussed gap size and their frequency near nests, although one paper reported that owls generally avoided nesting in gap areas in fire-restored forests in Yosemite (Roberts, 2008; Roberts et al., 2011). At larger scales (PACs and territories) gaps were still rare in the SEKI and Eldorado study areas (Table 3), and sparse in the Sierra and Tahoe areas, but we did not find any pattern suggesting their abundance or size class distribution was significantly different from conditions in the surrounding landscape. Owl tolerance of gaps is difficult to infer from our data because gaps of at least a dominant tree crown area or larger are rare in our study areas. Since spotted owls persisted in historic forests that had much lower canopy cover and more gaps than modern forests, a better understanding of owl response to gaps may require telemetry location data.

We found the cover in tall trees was the most important canopy feature in PACs from the surrounding landscape (Table 2). In contrast, several studies have found the percentage of moderately high (> 50%) and high (> 70%) levels of canopy cover were most associated with owl occupancy and reproduction (Berigan et al., 2012; Tempel and Gutierrez, 2013; Tempel et al., 2014; Tempel et al., 2015; Tempel et al., 2016). Across our four study areas, PAC canopy cover averaged 67.6% (Table 2), and on the three national forest study areas PAC canopy cover ranged from 3.9% (Sierra) to 21% (Tahoe) higher than the surrounding landscape (Table 3). However, our niche overlap analysis showed that the canopy structure that was most distinct (i.e., lowest niche overlap scores of 0.49–0.68) was the cover in tall trees (Table 2). Canopy cover had much higher niche overlap values (0.75–0.88) than other attributes. The confounding of high-levels of canopy cover with the cover of tall trees may explain why other studies that did not account for tree height have generally reported total canopy cover as the most significant feature of PAC habitat.

4.2. Variation in canopy conditions from nest site to landscape

While we found that total canopy cover was generally higher within about 500 m of nests (Fig. 4b) compared to the surrounding landscape, the area in tall trees continued to be the most distinct canopy structure (lowest niche overlap) as distance from the nest sites increased over the 1000 m from nests we assessed. This suggests that the cover in tall trees could also be beneficial to owls when foraging because they often travel away from the nest to forage (Irwin et al., 2007; Williams et al., 2011). However, without telemetry we were unable to assess how owls used different forest conditions for foraging. Several studies have suggested heterogeneous forest conditions, particularly edges between cover types, may influence foraging behavior or reproductive success (Franklin et al., 2000; Eyes et al., 2017). Some degree of vertical structure seems to be important for owl foraging (Call et al., 1992) but it's unclear whether owls respond to canopy layering produced by adjacent forest patches of contrasting height or multi-layer foliage within the same stand. New technologies such as lightweight GPS tracking devices could be used to pinpoint foraging locations and improve our analysis of vertical layering.

4.3. Study area differences in large tree abundance

We found that > 70% canopy cover was usually only achieved when there were tall trees present. Canopy cover in modern Sierra Nevada forests typically averages between 40 and 60% depending on several factors including forest type, site productivity and disturbance history (Lydersen and North, 2012; Miller and Safford, 2017). Forests with canopy cover > 70% are not rare, but they usually occur in mixed-conifer forest types and require a combination of high site productivity and/or a long period of fire suppression (Collins et al., 2011). The owl's documented association with high canopy cover conditions has raised one hypothesis that owls have benefited from fire suppression and may presently have more high-quality habitat than would have been present under active-fire forest conditions (North et al., 2017; Peery et al., 2017). However, if the preferred canopy characteristic of nest and PAC conditions is an abundance of tall trees, then large tree harvest, such as National Forests have experienced, may have reduced the quality and/or extent of favorable habitat on Forest Service lands.

We did not find significantly higher canopy cover levels in SEKI, the only owl study population that is not declining, but we did find significantly higher cover of tall trees. The covariance of many structural attributes in forests (i.e., old forests often have large trees, big snags and logs, etc.) makes it difficult to partition individual attributes as the most significant habitat variable. Cover of tall trees may directly benefit owls by providing overhead predator protection or microclimate modification or indirectly by being associated with other age, size, and dead wood structural attributes that often occur when tall trees are present (Gutiérrez et al., 1995). Our research shows that tall tree cover is correlated with owl habitat, but identifying the particular benefits will require further study.

4.4. Implications for future research

We acknowledge several limitations of our research that constrain our understanding of California spotted owl habitat but that might be addressed with future research. While our LiDAR analysis provides a large sample size and precise quantification of the forest canopy, it cannot provide information on snags and logs, either of which may influence habitat selection (Call et al., 1992; Verner et al., 1992; LaHaye et al., 1997). Methods are being developed to accurately assess snags using LiDAR, and understory conditions, including coarse woody debris, can be measured with ground-based LiDAR (Hopkinson et al., 2004). Ground-based methods will have smaller sample sizes than aerial LiDAR, however, stratified sampling of different structure classes may overcome these limitations.

We focused on partitioning elements of canopy conditions that usually co-vary. This required a large dataset of owl locations and their delineated PACs. A next step building upon our analysis would be to weight these locations either by their frequency of use (accounting for years of observation) or reproductive output. We also did not have spatially-explicit data of owl habitat use such as that derived from radio telemetry and therefore, beyond the nest site, we used general scales of PAC and territory. However, as a central place forager and as several telemetry studies have shown, owl use decreases with distance from nests or roost (Call et al., 1992; Carey and Peeler, 1995; Rosenberg and McKelvey, 1999; Blakesley et al., 2005; Irwin et al., 2007; Williams et al., 2011; Williams et al., 2014). We hypothesize that telemetry would likely show that owls typically have many areas within their territories that are lightly used or completely avoided (Carey et al., 1992). This would greatly refine an analysis of forest structural conditions associated with owl territories, which are predominantly used for foraging. The structural heterogeneity of forests that some studies have suggested may benefit owl foraging (Eyes et al., 2017) could be examined with a much better understanding of which parts of the territory areas are most heavily used. Better insight into owl territory use would also greatly benefit from a spatially-explicit sampling of small mammal abundance, particularly common prey species such as the dusky-footed woodrat (*Neotoma fuscipes*) and northern flying squirrel (*Glaucomys sabrinus*) (Ward et al., 1998; Smith et al., 1999; Meyer et al., 2005a; Innes et al., 2007; Meyer et al., 2007a) and how these prey species are affected by common forest treatments (Meyer et al., 2005b).

Finally, we do not infer what may constitute 'optimal' owl habitat. In three of our four study areas, forests have been extensively altered by past timber management and fire suppression. We have attempted to identify favorable habitat using areas in SEKI without timber harvest and having recently (i.e., since the 1970s) restored fire regimes. However, even these forests have higher density and canopy cover from pre-1970 tree ingrowth that is now large enough to survive re-introduced surface fire (Lydersen and North, 2012; Collins et al., in press). Our analyses may help identify favorable habitat under current conditions but this may be different from historical forests.

4.5. Management implications

Research on characterizing the structure of owl habitat has been constrained by both technological (aerial photography and landsat imagery) and logistical (ground-based vegetation measurement) issues. Early remote sensing efforts in owl studies has been limited to estimation of area, spatial configuration, and canopy cover whereas ground-based sampling provided limited estimates of density and sizes of habitat attributes at small spatial scales. All this previous research has linked spotted owls to a combination of high canopy cover and large trees at both nest and roost sites (Verner et al., 1992; Gutiérrez et al., 1995; Tempel et al., 2014, 2016). One consequence of these studies has been that managers have tended to focus on canopy cover as the metric of interest for conserving spotted owl habitat.

Two lines of evidence, one historical and one derived from our findings in this study, suggest that a focus on preserving patches of large trees rather than canopy cover per se may be more effective. Historical data sets and forest reconstruction studies from the Sierra Nevada consistently suggest active-fire forests on average were dominated by large trees and stands generally had low canopy cover (17–41%) and tree densities (60–328 trees/ha or 24–133 tree/ac) (Lydersen et al., 2013; Collins et al., 2015; Stephens et al., 2015). The range in these values suggests forest conditions likely varied with topography and disturbance history (North et al., 2009; Lydersen and North, 2012; Kane et al., 2014; Kane et al., 2015). More mesic sites likely burned less frequently and intensely, and higher productivity resulted in bigger trees in larger patches than more xeric sites. Fuels were able to accumulate more rapidly on more productive sites, especially when fires "skipped an area", making them more prone to patchy crown fire (Innes et al., 2006). Variability in topography and soils combined with the inherent variability of fire created and maintained high levels of heterogeneity at small to large spatial scales in historical frequent fire landscapes (Meyer et al., 2007b; Kane et al., 2015).

Management based on canopy cover targets creates significant challenges in restoring this multi-scale heterogeneity. Canopy cover is generally used as a stand average measurement of forest conditions and as such does not account for the group/gap horizontal distribution of trees that is a defining characteristic of frequent-fire forests (Larson and Churchill, 2012). Furthermore, because high canopy cover can occur under a wide variety of stand ages, levels of productivity, and disturbance histories, it does not incorporate important habitat components such as vertical structure, snags, downed logs, and large trees. Forests with high canopy cover, particularly those with continuous cover over large areas, are at greater risk from high-severity wildfire and drought-induced mortality. An additional challenge is that while canopy cover estimates of forest conditions are widely available, their calculation from ground-based measurements, aerial photo interpretation or model estimates such as FVS, based on tree diameters and density, can be widely variable and inaccurate (Fiala et al., 2006; Korhonen et al., 2006; Christopher and Goodburn, 2008; Paletto and Tosi, 2009).

In contrast, the association of owl nests and PACs with the cover in tall trees has more tractable forest management implications. Managing for the protection and production of large trees can be accomplished while still reducing potential fire intensity (through surface and ladder fuel reduction) and drought stress (lowering overall leaf area by removing small trees). Furthermore, PACs in our study had low canopy cover in the 2–16 m strata suggesting treatment of these potential ladder fuels may not adversely affect owl habitat. Reduction of subcanopy and intermediate-size trees may reduce water competition increasing large tree resilience to beetle attack while opening up more growing space to accelerate tree growth (Fettig et al., 2010a; Fettig et al., 2010b). Managing for landscapes that contain tall trees, which are more fire resilient, may reduce the loss of owl habitat that is increasingly occurring in an era of rising wildfire severity. In landscapes where patches of tall trees are rare, managers might identify the tallest tree areas and seek to reduce their vulnerability to drought and wildfire mortality through density reduction so the trees can grow to become anchors of more suitable habitat.

As a sensitive species with declining populations, forest managers should consider approaches to retain and improve California spotted owl habitat. Retaining current use areas is important to guard against further population declines. In the long-term an effective strategy may be to focus management on cultivating tall trees in more productive areas (i.e., wetter areas, drainage bottoms, lower slopes) of the landscape (Underwood et al., 2010) that can better support large tree biomass and that may be more resistant to fire and drought stress. This may take several decades and will require strategies that maintain current owl areas until new, more resilient forest locations develop large tree cover through growth and succession. To maintain selected habitat in the near-term, management may need to take a more active role reducing stem density in the 2–16 m class and surface fuels in tall tree areas to make these stands more resistant and resilient to drought and high-severity wildfire that can significantly reduce local owl populations (Jones et al., 2016). With climate conditions changing, managing for the retention and creation of large trees may benefit both owls and forest resilience to increasingly common wildfire and drought events.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2017.09.019.

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