



RESEARCH ARTICLE

Extent, configuration and diversity of burned and forested areas predict bat richness in a fire-maintained forest

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Abstract

Context Fire transforms, fragments and sometimes maintains forests, creating mosaics of burned and unburned patches. Highly mobile animals respond to resources in the landscape at a variety of spatial scales, yet we know little about their landscape-scale relationships with fire.

Objectives We aimed to identify drivers of bat richness in a landscape mosaic of forested and burned areas while identifying spatial scales at which bat

richness was most strongly related to extent, configuration, and diversity measures of landscape-level habitat.

Methods We used multi-species hierarchical occupancy modelling to relate bat richness to landscape variables at 10 spatial scales, based on acoustic data collected in the Sierra Nevada, United States. We also assessed redundancy among landscape variable type (extent, configuration, and diversity) and between focal patch types (forested and burned).

Results Bat richness was positively associated with heterogenous landscapes, shown by positive associations with pyrodiversity, extent and mean area of

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burned patches, burned and forested edge density and patch density and relationships were generally consistent across scales. Extent of forest cover and burned areas were highly correlated, but configuration and diversity of these patch types diverged.

Conclusions Bat communities of our study area appear to be largely resilient to wildfire and adapted to more heterogeneous forests and shorter-interval fire regimes that likely predominated before the fire suppression era.

Keywords Acoustic · Chiroptera · Hierarchical occupancy model · Pyrodiversity · Western united states · Wildfire

Introduction

Fires transform and fragment forests, creating mosaics of burned and unburned areas and interfaces between them (Lloret et al. 2002; Parkins et al. 2018). While effects of forest heterogeneity on wildlife have been comparatively well studied, we know much less about how the configuration of burned areas influences biodiversity (Kelly et al. 2012; Parkins et al. 2018). Highly mobile animals in particular, have the ability to move between burned and unburned patches and therefore may respond to landscape composition, configuration and diversity at multiple scales (Rocha et al. 2016; Tingley et al. 2016b; Nimmo et al. 2019). Limited research indicates that highly mobile animals may benefit from increased mobility and foraging opportunities afforded by fire edges (Eyes et al. 2017; Vanbianchi et al. 2017) but this is not consistent across species (Eby et al. 2013; Geary et al. 2019). Positive relationships between species richness and pyrodiversity have led to an increasing focus on managing landscapes with heterogeneous burn patterns (Sitters et al. 2014; Ponisio et al. 2016; Tingley et al. 2016b). However, translating this appreciation for the value of burn heterogeneity into regional management for highly mobile species will require understanding the aspects of burned area configuration to be managed and the appropriate scale for management as well as underlying drivers of biodiversity-fire relationships (Swan et al. 2015; Kelly and Brotons 2017; Nimmo et al. 2019).

Insectivorous bats are highly mobile predators that respond to forest structure and fire based on their diverse call and morphological traits (Schnitzler et al. 2003; Denzinger and Schnitzler 2013; Blakey et al. 2019). At fine spatial scales (≤ 500 m), bats adapted to open areas and many edge-adapted species benefit from higher burn severity and more frequent fire (Armitage and Ober 2012; Buchalski et al. 2013; Inkster-Draper et al. 2013; Cox et al. 2016; Blakey et al. 2019; Steel et al. 2019). Bats also use edges and openings created by timber harvest (Law et al. 2016b and references therein). Clutter-tolerant species may be negatively associated with forest openings and burned areas, but the evidence is not consistent across studies (Law and Chidel 2002; Morris et al. 2010; Webala et al. 2011; Buchalski et al. 2013; Cox et al. 2016; Silvis et al. 2016; Blakey et al. 2019). Openings and edges can act as movement corridors, connecting habitat patches (Kalcounis-Rueppell et al. 2013) or provide high quality foraging habitat (Malison and Baxter 2010; Gonsalves et al. 2012), by combining ease of flight and echolocation in open space with abundant prey in cluttered vegetation along edges (Arrizabalaga-Escudero et al. 2015).

Bats respond to habitat features at different spatial scales (Perry et al. 2008; Mendes et al. 2017; Starbuck et al. 2020). At a fine scale (< 100 m), habitat use is often driven by prey abundance or fine-scale habitat structure such as presence of water or edges (Morris et al. 2010; Müller et al. 2012; Blakey et al. 2017a). At home range scales (> 500 m), habitat use may be influenced by the extent or configuration of resources (forest, edge, open areas, roost networks, water) (Lookingbill et al. 2010; Johnson et al. 2012; Fuentes-Montemayor et al. 2017). A study in California showed that, when considered together, bat captures increased as the density of forest edge within 1.5 km increased (Duff and Morrell 2007). In agricultural systems of Europe, bat richness and overall activity increased with proximity to forest edges (Heim et al. 2015). Although high levels of habitat fragmentation can reduce bat richness and activity, for example in urban or agricultural settings (Hale et al. 2012; Russo and Ancillotto 2015; Mendes et al. 2017), heterogeneity of vegetation also may positively influence bats at the landscape scale by increasing edge density (Klingbeil and Willig 2009). The scale at which bats respond most strongly to habitat varies with their mobility, as well as morphological and call traits (Farneda et al.

2015; Fuentes-Montemayor et al. 2017), leading to scale-dependent relationships between landscape structure and bat richness (Mendes et al. 2017). To date, landscape-scale effects of fire on bat communities have included investigation of the extent of high severity burned area at 2 km scale (Buchalski et al. 2013), burn severity and pyrodiversity at scales ≤ 500 m (Steel et al. 2019) and burn severity at scales from 90 m to 5,760 m (Starbuck et al. 2020). The landscape diversity and configuration of burned and forested areas have not been investigated simultaneously and the influence of the configuration of burned areas on bat communities remains unstudied.

We studied how bat richness varied in response to five landscape variables representing extent, configuration, and diversity of burned and forested areas. Our aim was to better understand the complex relationships among forest cover, fire, and diversity of highly mobile animals. We chose to investigate forested areas alongside burned areas because previous studies have provided evidence that changes to vegetation structure are key to mammal response to fire (Swan et al. 2015; Blakey et al. 2019). We aimed to identify drivers of bat richness in a landscape mosaic of forest and burned areas, identifying the spatial scale at which bat richness is most strongly related to extent, configuration and diversity measures of landscape-level habitat and assessing redundancy among landscape variables. We made six specific predictions (Table 1).

Methods

Study area

We surveyed bats in Plumas National Forest (4638 km²), which encompasses part of the Sierra Nevada mountain range in northern California (40°00'01"N 120°40'05"W, Fig. 1). Elevations within the Forest range from 311 to 2433 m, mean annual rainfall is high for the state of California (1036 \pm 306 mm), and mean temperature is 10.1 \pm 0.9 °C (1895–2017; Western Regional Climate Center 2017). Dominant vegetation includes lower and upper montane forest such as ponderosa pine (*Pinus ponderosa*) mixed conifer, white fir (*Abies concolor*) mixed conifer and red fir (*Abies magnifica*) forest, interspersed with meadows and montane chaparral (Fites-Kaufman et al. 2007). The forest has experienced seven particularly large (>

20,000 ha) wildfires occurring since 2000. The study area was not highly fragmented at the time of the study, with 66% forest cover, 11% open (treeless) unburned areas, 14% burned forested areas and 9% both burned and open areas (USDA Forest Service 2017, 2019). However, this structure may not reflect a historical state, as recent Northern Sierra Nevada vegetation structure (2005) is likely to have greater cover of dense forest, larger patch sizes, and more homogeneous vegetation structure than historical vegetation prior to widespread timber harvesting (1941) (Lydersen and Collins 2018).

Bat surveys

We surveyed bats acoustically and analyzed bat calls using methods described in detail in Blakey et al. (2019) and briefly summarized here. We sampled 83 randomly selected sites within Plumas National Forest, recording echolocating bats using Pettersson D500x bat detectors (Pettersson Elektronik, Uppsala, Sweden) over three spring-summer periods, corresponding to bat lactation season and the period of greatest bat activity. Within these periods, sampling was conducted between 8 June and 31 July 2015, 31 May–8 August 2016 and 12 June–24 July 2017 and individual sites were not revisited in multiple years. As year (2015, 2016, 2017) was not a significant predictor of bat species occupancy in a previous study using the same dataset (Blakey et al. 2019), we did not include it in our models. We visited each site once and placed a bat detector with the microphone elevated to 2 m to record from before sunset to after sunrise (7:30 pm–6:30 am) for three consecutive nights. We used automated acoustic analysis software (*SonoBat* 4.2.2, SonoBat, Arcata, CA, US) to identify bats to species (where possible). We used the *SonoVet* tool to manually check calls that had been identified to species by the software to ensure a high level of confidence in the identifications (Russo and Voigt 2016). A species was recorded as “detected” when at least one call was of sufficient quality with diagnostic characteristics for confident identification; detection was recorded for each night separately.

Focal patch types (forested and burned areas)

We calculated extent of forest cover and burned areas (proportional cover of all forested or burned patches

Table 1 Description and justifications for predictions of this study

Prediction	Justification
a. Bat richness is more strongly related to forest cover variables than fire variables.	Previous work in the study area indicated that forest structure is a key driver of the relationship between bats and fire in fire-prone coniferous forests (Blakey et al. 2019)
b. Bat richness is more strongly related to configuration of forest cover than extent of forest cover	Given bats have strong associations with edges and gaps (Loeb and O’Keefe 2011; Gonsalves et al. 2012), it is likely that configuration, rather than proportion of forest will likely be more important for maintaining a diverse community
c. Bat richness increases with increasing vegetation structural diversity and pyrodiversity and these relationships will be consistent across scales.	Given bats respond in varying ways to forest structure, according to their traits (Blakey et al. 2017b), it is likely that a variety of structures will likely host the greatest number of bats. Similarly, at the site-scale, bat species of coniferous forests respond differently to fire (Buchalski et al. 2013; Blakey et al. 2019) indicating that greater pyrodiversity will result in more species
d. Bat richness is negatively related to forest cover continuity at finer scales and positively related to forest cover continuity at broader scales; richness is positively related to burned area continuity at finer scales and negatively related at broader scales.	While edges and gaps are important features for foraging bats at finer scales (Loeb and O’Keefe 2011; Gonsalves et al. 2012), excessive fragmentation of habitat is likely to reduce species richness (Trubitt et al. 2019)
e. Landscape extent and configuration variables are highly correlated across scales.	Landscape extent and configuration variables are often reported to be correlated in the literature (Andren 1994)
f. Forest and burned area variables are highly correlated across scales.	Fire can transform landscape structure, creating edges and openings, this is particularly so for high severity fire, which is common in the study area

Predictions a-d relate to relationships between landscape variables and bat richness and predictions e-f relate to redundancy among landscape variables

within buffer) at 10 spatial scales defined by 10 concentric buffers of 1–10 km radius around each study site (Fig. 1c, d). Given the number of sites ($n = 83$), within the 4638 km² study area, some buffers overlapped, and this overlap increased with buffer radius. Median number of buffers overlapping with each site ranged from 0 at 1 km to 12 at 10 km and proportion overlap (the mean across each site’s overlap with its maximum overlapping site) was 0.10 ± 0.01 SD (1 km) and 0.77 ± 0.02 (10 km). To assess how increasing overlap among buffers may influence characterization of our landscape over and above inherent spatial autocorrelation, we compared variograms of our sites (all 10 buffers), with a set of 25 sites evenly spaced 20 km apart across the study area to provide non-overlapping buffers from 1 to 10 km (Fig. S1, Supplementary material). We found that at larger buffer sizes, the relationships between site similarity and distance between sites appeared similar across our study buffers and the non-overlapping

buffers, giving us confidence that increased similarity between sites at larger buffer sizes is due to a broader sample of the landscape, rather than increased overlap (Fig. S1). To calculate forest cover, we first extracted canopy cover from vegetation mapping polygon data (USDA Forest Service 2019) based on the CALVEG (“Classification and Assessment with Landsat of Visible Ecological Groupings”), which has an approximate grain size of 30 m (Nelson et al. 2015) and was developed from source data from 2000 to 2014 (USDA Forest Service 2019) (Fig. 1a). We discovered that not all fires had been updated within the dataset; vegetation source data was from a time period that preceded 25 fires occurring between 1996 and 2015, this area represented 7% of the study area. As a full revision of the vegetation dataset was out the scope of this study, we visually inspected maps of the high severity patches of these 25 fires and confirmed that they largely represented open areas at the time of the study, using 2016 one meter National Agriculture Imagery

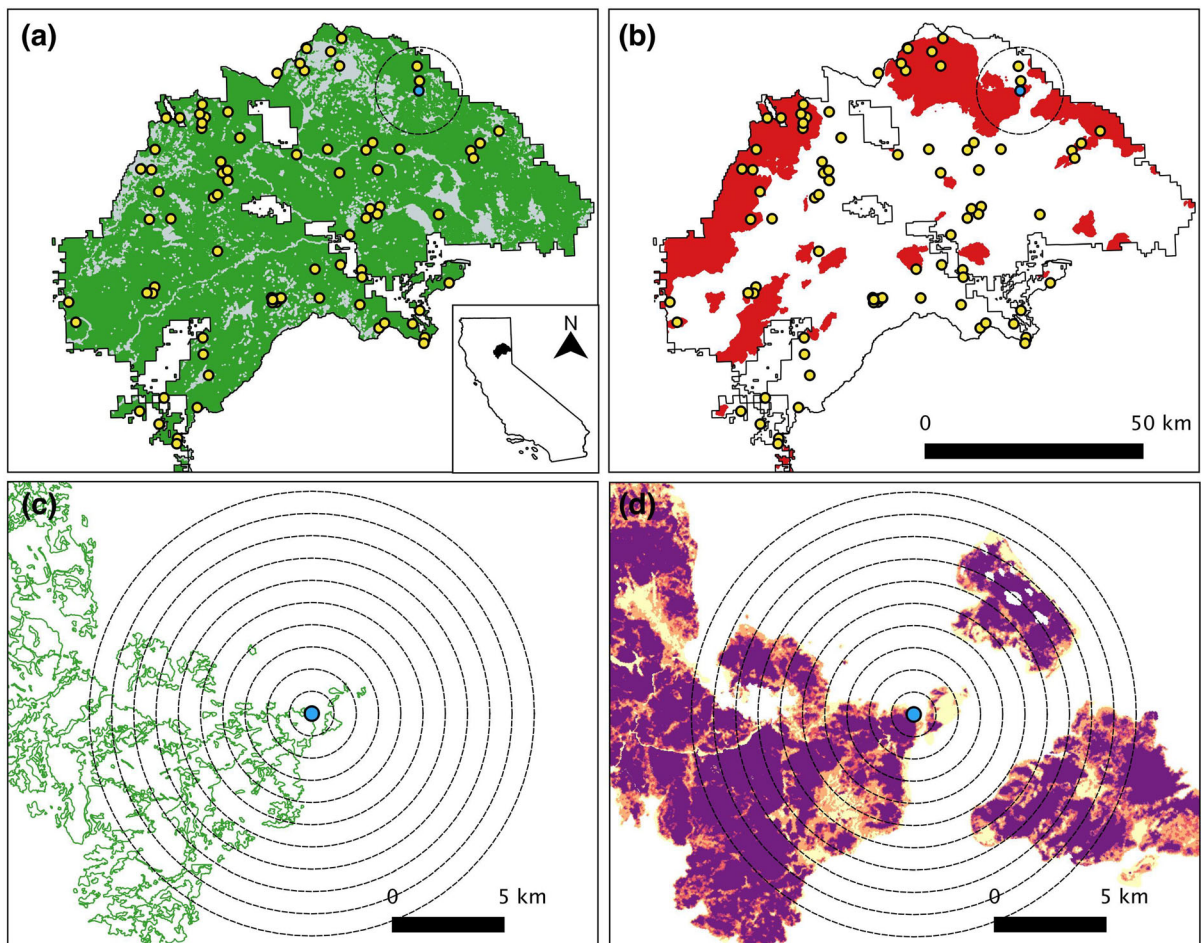


Fig. 1 Bat acoustic sampling sites (circles, $n = 83$) within Plumas National Forest in the Sierra Nevada mountain range, Northern California, USA (see inset). Maps show the National Forest boundary with (a) forested (green) and open (grey) areas, and (b) areas burned between 1987 and 2015 (red) and unburned during those years (white). Panels (c) and (d) show 10 concentric 1-km buffers around a single site (blue circle), the

location of which is indicated in panels (a) and (b) with a blue point and dashed 10-km buffer circle. Panel (c) shows forest edges (green lines) used to calculate edge density and panel (d) shows variability in maximum burn severity from high (purple) to low (yellow), the standard deviation of burn severities was used to represent pyrodiversity; see [Methods: Focal Patch Types \(Forested and Burned Areas\)](#).

Program (NAIP) imagery to check vegetation structure. We then classified areas within our vegetation data overlapping with these high severity polygons as zero canopy cover. We characterized open areas as zero canopy cover areas and forest as non-zero canopy cover areas, while edge was the boundary between these two categories (Fig. 1c). Burned areas were defined as any areas that had burned between 1987 and 2015, using a USDA Forest Service (2017) canopy burn severity (hereafter “burn severity”) dataset (Fig. 1b). The burned edge was defined by the boundary between burned areas (of any severity) and unburned areas (those that had no recorded fires since

1987). The number of detectors was not balanced between unburned and burned sites ($n = 28$ burned, $n = 55$ unburned) because sites were selected as part of a Forest Service monitoring program with multiple goals. However, we were most interested in the relationships between bats and the broader burned landscapes and burn configurations varied substantially across the sites. Three small fires burned within the study area during the study (2015–2017), which we consider unlikely to affect study findings because although their burned area overlapped with five site buffers, these were restricted to the 10 km buffer zones

(> 9 km from sites) and overlapping areas were < 0.1 % (0.01–0.06 %).

In addition to extent, we calculated three configuration variables for forested and burned areas within each buffer—mean patch area (mean of individual patch areas), patch density (number of patches divided by buffer area), and edge density (edge distance divided by buffer area)—and one diversity variable (details below). We converted forest cover and burned area spatial layers to rasters (30 m resolution) and used *FRAGSTATS* (McGarigal 1995) within the *SDMtools* v1.1-221 package to calculate the three configuration variables at each of the 10 buffer distances for each site.

We estimated vegetation structural diversity by taking the standard deviation of canopy cover across all pixels within each buffer, using vegetation data (USDA Forest Service 2019) based on the CALVEG (“Classification and Assessment with Landsat of Visible Ecological Groupings”) classification (Nelson et al. 2015) for all vegetation variables. To estimate pyrodiversity (Fig. 1d), we calculated the standard deviation of burn severity across all pixels within each buffer (Tingley et al. 2016b). Burn severity was the maximum burn severity value recorded since 1987, expressed as a value ranging from 0 to 5, where classes 0–5 indicate 0 = unburned, 1 = burned but no change in canopy, $2 \leq 25$, $3 = 25\text{--}50$, $4 = 50\text{--}75$, $5 \geq 75$ % canopy cover loss using burn severity spatial data (USDA Forest Service 2017).

Relationships among landscape variables

We had two objectives when investigating relationships among predictor variables (Table 1, predictions e–f). The first was to investigate the degree of correlation (Pearson’s correlation coefficient) between variables representing the extent of each focal patch type (forest or burned area) with variables representing configuration of patches or diversity. Given strong effects of fire on vegetation structure, the second objective was to establish the degree of correlation between these same variables (extent, configuration, and diversity) when calculated for forested versus burned areas. For both of these objectives, we were interested in the effects of spatial scale, specifically grain size, on variable associations, so correlations were calculated at each of the 10 buffer distances.

Relationships between bat richness and landscape variables

We made four predictions about relationships between bat richness and landscape variables (Table 1a–d) which we investigated using multi-species hierarchical occupancy modelling (Kéry and Royle 2008) following methods described in detail in Tingley et al. (2016b). We chose an occupancy approach because bat detectability during acoustic studies varies greatly among species and with environmental factors (Rodhouse et al. 2012; Banner et al. 2018). We assumed our observed data ($y_{i,j,k}$) were imperfect observations of the true unobserved occupancy state of species i at site j ($z_{i,j}$) where detection or non-detection of species i at site j on night k conformed to a Bernoulli distribution, such that:

$$y_{i,j,k} \sim \text{Bernoulli}(p_{i,j,k} \times z_{i,j})$$

For all models, we modelled detectability as a function of three uncorrelated covariates, daily maximum ($\text{max}T$) and minimum ($\text{min}T$) temperatures and moon illuminated fraction (moon), which were found to be important predictors of bat detection variability within the study area (Blakey et al. 2019). We modelled the probability of detecting bat species i at site j on night k ($p_{i,j,k}$) as the logit-linear function of the three detection covariates:

$$\text{logit}(p_{i,j,k}) = \alpha_0 + \alpha_1 \text{max}T_{j,k} + \alpha_2 \text{min}T_{j,k} + \alpha_3 \text{moon}_{j,k}$$

We fit separate multi-species occupancy models for each landscape variable ($n = 5$; extent, mean patch area, patch density, edge density, diversity) and each buffer distance ($n = 10$; 1–10 km) for both forested and burned areas ($n = 100$ models). For each model, the landscape predictor (e.g. extent of forest cover at 1 km buffer distance) was the sole predictor of multi-species occupancy probability. We expected the true occurrence state of $z_{i,j}$ to follow a Bernoulli distribution such that:

$$z_{i,j} \sim \text{Bernoulli}(\psi_{i,j})$$

We modeled occupancy probability for species i at site j as a logit-linear function of the covariate of interest (var), for example: extent of burned area at buffer size of 5 km.

$$\text{logit}(\psi_{i,j}) = \beta_0 + \beta_1 \text{var}_j$$

We did not include temporal variables as occupancy covariates (e.g. day of season, year), because these variables were not found to be significant predictors of occupancy of the 9 most common bat species in the study area (Blakey et al. 2019). We fitted Bayesian hierarchical models using vague priors (normal: $\mu = 0$, $\tau = 0.01$, gamma: $r = 0.1$, $\lambda = 0.1$) and estimated model parameters with 3 Markov-chain Monte Carlo simulations with 5000 burn-in iterations and sampled the posterior for 5000 iterations thinned by every 5th iteration. This process yielded 3000 posterior samples. To ensure model convergence, we checked trace plots and verified that all R-hat values were < 1.1 . We assessed residual spatial autocorrelation by first extracting the residuals (or “discrepancy”) for each model by subtracting occupancy probability ($\psi_{i,j}$) from occupancy state ($z_{i,j}$) for each species in each of the 3000 draws from the posterior sample (Wright et al. 2019) and then applying the Moran’s I test to each species in each model. We then calculated the proportion of iterations for each model that resulted in a rejection of the null hypothesis that there was zero spatial autocorrelation in the residuals at $\alpha = 0.05$ (evidence for significant spatial autocorrelation unaccounted for by the model). We fitted models with the JAGS program (Plummer 2003) within the R statistical programming language (R Development Core Team 2019) with the *jagsUI* v1.5.1 package (Kellner 2019). Model code was developed from JAGS code used in Tingley et al. (2016b), available online at (Tingley et al. 2016a).

We used the posterior sample of the hyperparameters (community-level parameters) at each scale and used these to interpret the magnitude and direction of the relationship between bat occupancy at the community level and the variable of interest. Given that hyperparameters are in essence the average effect of each variable across all species modeled, they should be highly correlated with the effect of a variable on richness.

To graph the predicted relationships between bat richness and our landscape variables, we fit separate generalized linear models (GLMs) with a Poisson distribution and log link to each of the 3000 posterior samples of the true occurrence state ($z_{i,j}$) for all bat species from each of the 100 models. We used estimated richness (sum of all species predicted to

occur) as a Poisson-distributed response variable (with log link) and the landscape variable as the predictor. We calculated the mean and 95% Bayesian credible intervals for predicted richness values across all iterations for the range of the predictor variable to interpret modelled relationships. We interpreted significant relationships as those where credible intervals of modelled coefficients did not overlap zero.

Results

Scale-Dependent relationships between bat richness, forest cover and burned areas

Our final bat dataset spanned 249 survey nights (83 sites for three nights each). Bat species recorded included 17 species: *Myotis californicus* (69 nights detected); *M. evotis* (61); *Lasionycteris noctivagans* (44); *Eptesicus fuscus* (35); *Tadarida brasiliensis* (31); *M. lucifugus* (24); *Lasiurus cinereus* (24); *M. thysanodes* (20); *M. yumanensis* (16); *Antrozous pallidus* (16); *M. volans* (15); *L. blossevillei* (8); *M. ciliolabrum* (4); *Corynorhinus townsendii* (4); *Parastrellus hesperus* (3); *Euderma maculatum* (2); *Eumops perotis* (2). Bat richness decreased with increasing extent of forest cover and mean forest patch area and increased with increasing extent of burned area and mean size of burned patch across all scales (Figs. 2 and 3). Patch and edge density were positively associated with bat richness for forest cover across scales, but with burned areas only at finer scales (Figs. 2 and 3). Bat richness increased with pyrodiversity but was unrelated to vegetation structural diversity (Fig. 2).

As predicted (Table 1a), forest cover variables were stronger predictors of bat richness than were burned area variables (Figs. 2 and 3). However, contrary to our predictions, extent variables tended to have similar or larger effect sizes compared to configuration and diversity variables (Table 1b and Fig. 3). While bat richness increased with pyrodiversity as expected, there was no evidence that bat richness increased with vegetation structural diversity (Table 1c and Figs. 2 and 3).

We found limited support for our prediction that bat richness would be negatively related to forest cover continuity at finer scales and positively related to forest cover continuity at broader scales, and the inverse for burned areas (Table 1d). Instead, bat

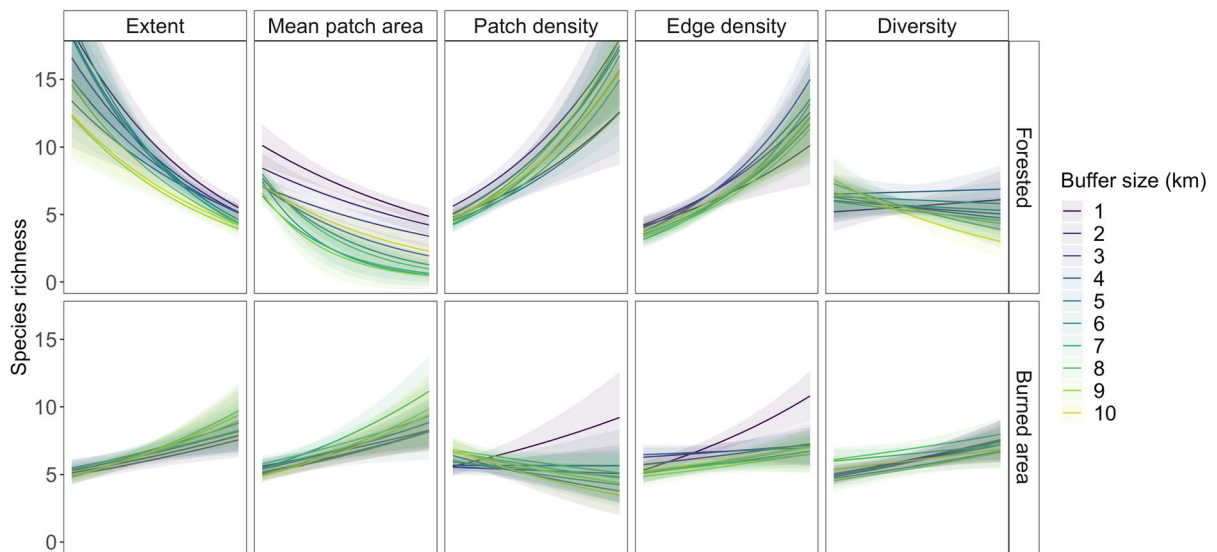


Fig. 2 Relationships between bat richness and 5 landscape variables for both forest cover (top) and burned area (bottom) across 10 buffer distances (1–10 km) based on generalized linear models (GLMs) relating predicted bat richness from multi-species occupancy models (y axis) to landscape variables

(x axis). All landscape variables have been scaled and centered at each buffer distance to facilitate comparison of strength of relationships (x-axes are not labelled for this reason). Diversity refers to vegetation structural diversity (top) and pyrodiversity (bottom)

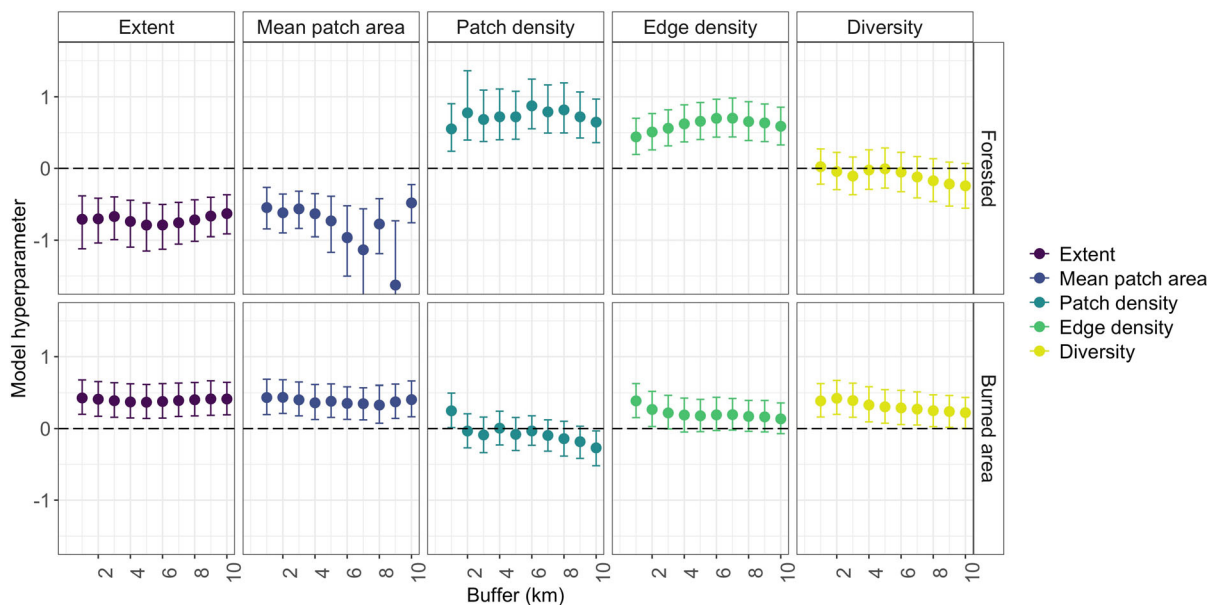


Fig. 3 Hyperparameter estimates (community effect) from multi-species occupancy models with 95 % Bayesian credible intervals representing effect size of modelled relationships

richness was negatively related to forest cover continuity (negatively related to mean patch area and forest cover extent, positively related to patch density and edge density) across all scales from 1 to 10 km (Figs. 2

and 3). Similarly, bat richness was positively related to burned extent and mean patch area across all scales (Fig. 3). The only support we found for the prediction that bat richness would be positively related to burned

area continuity at finer scales and negatively related to burned area continuity at broader scales was the relationship between richness and patch density, which varied in this direction (Table 1d and Fig. 3). Otherwise, strength of relationships between bat richness and landscape variables were generally consistent across spatial scales (Figs. 2 and 3; Fig. S2). Our assessment of residual spatial autocorrelation in our models showed that there was spatial autocorrelation in residuals for the majority of iterations (80 % of models, mean proportion of iterations = 0.572 (0.466–0.804)) for one of the 17 species (*M. evotis*). For the remaining 16 species, the proportion of iterations showing spatial autocorrelation in residuals was much lower (mean = 0.053 (0.004–0.194)). We therefore consider that spatial autocorrelation may have influenced our results by underestimating variance, but it is unlikely that spatial autocorrelation invalidates our results.

Is there redundancy among extent, configuration, and diversity measures of landscape-level habitat?

Associations between landscape variables varied with focal patch type (forested or burned) and sometimes also with spatial scale (1–10 km) (Fig. 4). In contrast to our predictions (Table 1e), extent of forested area was highly correlated ($|r| > 0.7$) with only one other forest variable across all scales (patch density; negatively) and highly positively correlated with mean forested patch area only at finer scales (< 3 km, Fig. 4a). However, extent of burned area was highly positively correlated with mean burned patch area, pyrodiversity, and edge density at all scales and with patch density at the finest (1 km) scale, consistent with our predictions (Fig. 4b). Also in contrast to our predictions (Table 1f), forest cover and burned area variables were not highly correlated with one another, only extent of forest cover and burned area were negatively correlated by $|r| > 0.6$ across all scales (Fig. 4c). Among configuration variables, burned area variables were more strongly correlated to one another, with all variables highly correlated ($|r| > 0.7$) at the finest scale (1 km), while edge density, pyrodiversity, and mean patch area were also highly correlated at 2 km and edge density, and pyrodiversity were highly correlated across all scales. Among forest cover configuration variables, edge density was highly correlated with patch density and mean patch area at the finest scale (1 km) and also at

the broadest scale (10 km) but no strong correlations occurred in the intermediate scales.

Discussion

Our study revealed new insights into landscape-scale habitat relationships of mobile species in fire-affected forests. We found mixed support for our predictions, finding evidence for stronger relationships between bat richness and forest structure as compared to fire (Table 1a) but little evidence for stronger relationships between bat richness and configuration, rather than extent variables (Table 1b). While we found evidence that pyrodiversity increases bat richness across all spatial scales, we found no evidence that forest structural diversity, as measured in our study, influenced bat richness (Table 1c). We found little support for the prediction that relationships between bat richness and landscape variables varied across scales (Table 1e) and while forested and burned area extents were highly correlated, configuration variables were not correlated between the two focal patch types (Table 1f).

Bat richness was strongly predicted by extent and configuration of forest cover across scales, such that patchier forest, with high edge density and lower overall cover, resulted in the highest bat richness. In this way, our study is consistent with previous studies showing that bats are resilient to or may even benefit from a degree of forest heterogeneity (Bernard and Fenton 2007; Klingbeil and Willig 2009) while at odds with studies showing negative effects of heterogeneity on bat communities (Fenton 1992; Ferreira et al. 2017). Negative relationships between forest continuity and bat richness were consistent across scales, at odds with our predictions. This may be because the bat community of our study area is adapted to historically more heterogeneous forests and relatively short-interval fire regimes (Steel et al. 2019). Present-day forests of the Northern Sierra Nevada are likely to have greater forest continuity and extent of dense forest than they did historically (Lydersen and Collins 2018). Similarly, due to fire suppression and climate change, modern fire regimes are less variable than historically (Cansler and McKenzie 2014; Safford and Stevens 2017), with an increase in larger and more homogeneous high severity burned patches (Steel et al. 2018). The positive relationships we found between bat

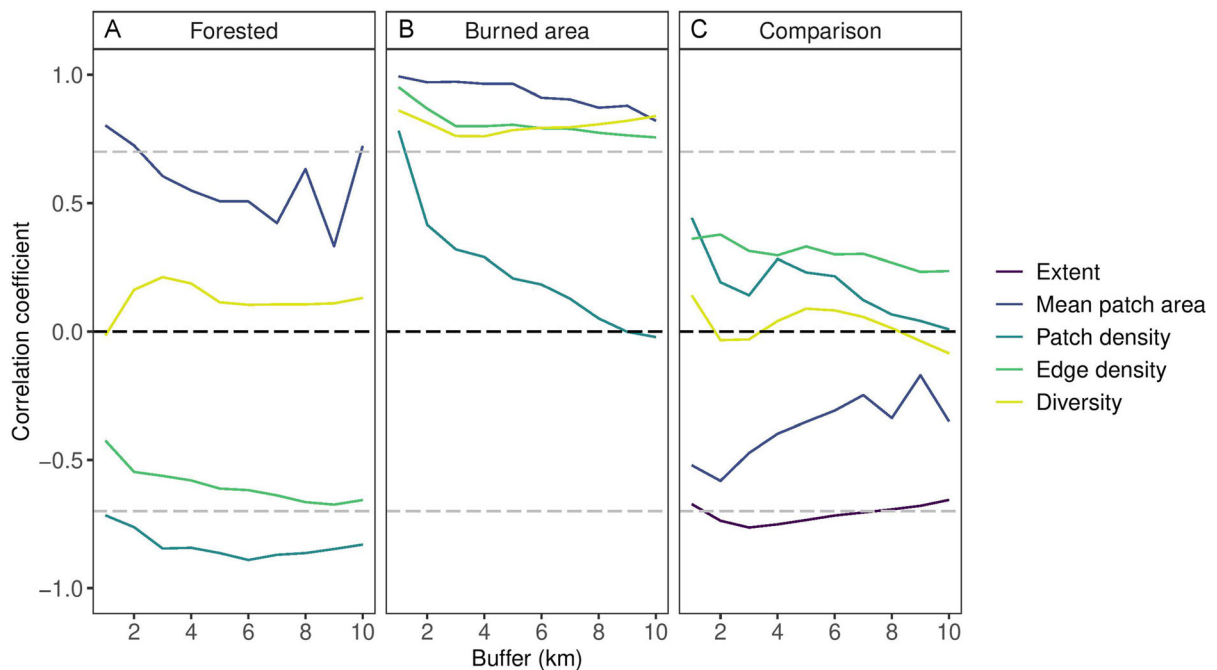


Fig. 4 Associations between landscape variables examined in this study at different spatial scales. Panel A shows correlations between extent of forest cover and configuration/diversity variables (mean patch area, patch density, edge density, and vegetation structural diversity) at buffer scales ranging from 1 to 10 km. Panel B shows the same relationships for burned area

(correlations between burned area extent and configuration/diversity variables) and Panel C (“Comparison”) shows the correlations between the same variables measured for both forest and burned area. Grey dashed lines show $|r| = 0.7$, an indicator of when variable collinearity may distort model estimation (Dormann et al. 2013)

richness, burned area extent, burned patch size and edge density, along with other studies showing high resilience of bat communities in Western forests to fire, also indicate that bats of the region may be adapted to shorter fire intervals (Buchalski et al. 2013; Steel et al. 2019; Starbuck et al. 2020). We may expect the negative relationship we observed between bat richness and forest cover to become positive after a threshold of forest fragmentation due to fire or other mechanisms, given positive relationships that have been demonstrated between bats and vegetation cover in agricultural, urban (Threlfall et al. 2011; Bailey et al. 2019), and fragmented tropical landscapes (Rocha et al. 2016). While the shift in the relationship between bat richness and burned patch density from positive at the finest scale (1 km) to negative at the broadest scale (10 km), may provide initial support for this prediction, further study is needed to establish thresholds of heterogeneity for bats in burned landscapes.

Our result that pyrodiversity was positively associated with bat richness across landscape scales

supports findings that bat richness increases with pyrodiversity at finer scales (500 m) (Steel et al. 2019), likely due to variable responses to burned area characteristics by bat species (Starbuck et al. 2020) with different ecological and morphological traits (Blakey et al. 2019). Interestingly, pyrodiversity was not correlated with vegetation structural diversity, which was unrelated to bat richness. This finding suggests that factors additional to forest structure are likely influencing bat community response to burned landscapes, potentially including booms in prey productivity (Malison and Baxter 2010) or gradual ecotones between forests and open areas, providing habitat for diverse bat guilds and maintained by mixed-severity fire (Broken-Brow et al. 2019). Discrepancies between the fire and vegetation datasets in timing and accuracy may also have influenced the lack of correlation between the pyrodiversity and vegetation structural diversity and lack of a relationship between bat richness and vegetation structural diversity.

Several limitations are important to consider when interpreting our results that may also be productive areas for future study. First, the burned areas assessed in our study represented a variety of different fires which burned since 1987 and encompassed a range of severities, which could partially explain the lower than expected correlations between burned and forested configurations and could influence relationships between bat richness and landscape variables given both burn severity and time since fire have been shown to influence bat occurrence (Blakey et al. 2019; Steel et al. 2019; Starbuck et al. 2020). To partially assess the importance of this variability in fire regime, during the exploratory stage we ran models using only high severity burned areas to calculate the landscape extent and configuration variables and recorded similar modelled relationships. The variability among burned areas included in this study likely masked some of the more subtle relationships between bats and burned areas in space and time, especially because two species in the study area have exhibited site-scale relationships with time since fire at finer scales (Blakey et al. 2019). Further, our measures of occupancy are based on acoustic data and therefore do not provide information about other important aspects of bat response to fire, including: roost habitat for bats, which may be a limiting factor, particularly during the maternity period (Kunz et al. 2003); or reproductive rates, which may be reduced following fire (Ancillotto et al. 2020). Finally, we approximate forest cover and burned area edges based on mapped extent of forest cover and burned areas and do not differentiate between gradual and abrupt edges, which may influence bat habitat use (Broken-Brow et al. 2020). While bat communities appear to be resilient to or even benefit from some degree of forest heterogeneity at landscape scales in coniferous forest, it is important to remember that many individual bat species require forest cover or unburned areas for commuting, roosting, and foraging (Henderson et al. 2008; Snider et al. 2013; Threlfall et al. 2013; Law et al. 2016a).

Conclusion

Our study has implications for natural resource managers and landscape ecologists who seek to conserve or understand highly mobile animal

communities in fire-maintained coniferous forests. Prior to European colonization, the northern Sierra Nevada bat community existed within a mixed-severity fire regime that maintained a mosaic of patches on the landscape through frequent low- to moderate-severity wildfire (Van Wagtendonk and Fites-Kaufman 2018). Forest management directed at simulating vegetation patterns maintained by wildfire (i.e., pyrodiversity) has been proposed in the Sierra Nevada to reduce the risk of broad-scale stand-replacing wildfire (Sherlock 2007; North et al. 2009), and using this approach to restore habitat patch size, structure and configuration to a natural range of variation will likely benefit bat communities. Management practices directed at restoring bat diversity could benefit from concomitant consideration of species-specific habitat needs. For example, conservation concerns have been raised for six of 17 bat species on this landscape, and five of these six species are adapted to foraging in structurally complex vegetation (late-seral forest; Blakey et al. 2019). On this landscape, a combination of maintaining existing late-seral forest while incorporating wildland fire use (van Wagtendonk 2007) and/or implementing vegetation treatments that replicate patterns maintained by frequent mixed-severity fire (i.e., pyrodiversity) in mid-seral forest (e.g. North et al. 2019) could maintain habitat for clutter-adapted species while restoring fire-maintained conditions across the landscape and promoting bat diversity.

For landscape ecologists, we found independent relationships between bat richness and configuration of forested and burned areas. We showed that in fire-maintained coniferous forests, even when extent of forest cover and burned areas are correlated, configuration and diversity of these metrics may diverge. Relationships between bat richness and landscape variables were relatively consistent across scales, similar to Starbuck et al. (2020). However, further study is needed to investigate thresholds of heterogeneity for bats in burned landscapes, particularly in regions where wildfires are increasing in frequency and extent (Dennison et al. 2014).

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Data accessibility Bat detection data are archived on the USDA Forest Service Nature Resource Information System (<https://www.fs.fed.us/nrm/index.shtml>) and also on the Bat Acoustic Monitoring Portal (BatAMP): <https://batamp.databasin.org/datasets/65ce65a3c3ed4672a3d14aba5ef90677> (2015); <https://batamp.databasin.org/datasets/fe446554eb31429d8c14462e3c3e0d4a> (2016); and, <https://batamp.databasin.org/datasets/db15f5ee4dd7462fa6d1d1097e41656a> (2017).

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