Bat occupancy in Sierra Nevada wildfire areas and implications for post-fire forest management

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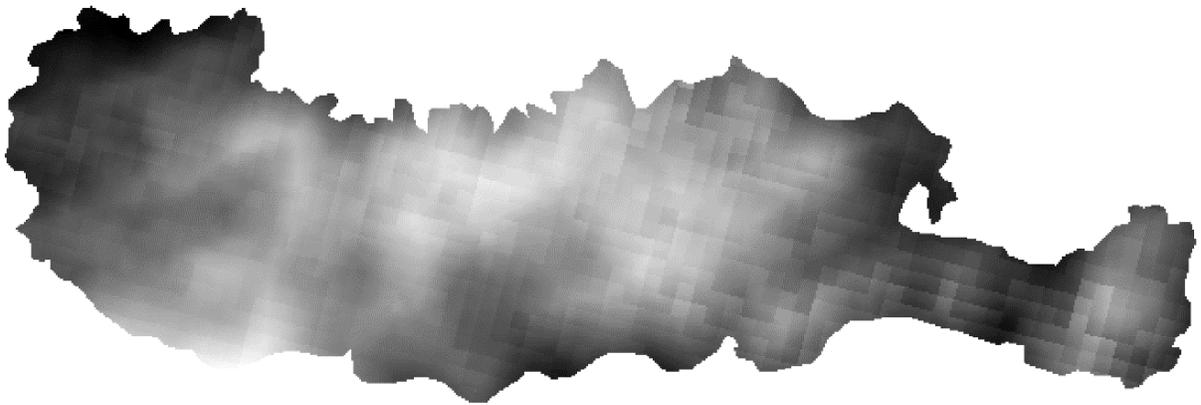
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Abstract

During 2014-2017 acoustic bat monitoring was conducted in and around the 2004 Power Fire, 2012 Chips Fire, and the 2013 Rim Fire areas using automated recording units. In total, 331 unique locations (accounting for 2091 survey-nights) were monitored, including sites outside of the burn perimeter, located across the burn severity gradient, and within areas managed for reforestation and left unmanaged. This report details analyses conducted using these data to inform post-fire management within the study fires as well as within future burn areas. Two groups of species occupancy models were built for twelve Sierra Nevada bat species. The first set of models utilized landscape-scale environmental data, and are the basis for FIRE-BAT, a geographic information system (GIS) toolbox for producing spatially-explicit predictive maps of bat occurrence in Sierra Nevada wildfire areas. The second group of models used stand-level field-collected data to evaluate bat species associations with forest structure characteristics, which are directly altered by wildfires and forest management. These models were applied to four scenarios of forest habitat conditions representing contrasting successional stages and hypothetical management targets.

The relevance of individual environmental factors to bat occupancy varied between models, indicating individual species respond to habitat conditions idiosyncratically. However, some generalities were also evident. With varying degrees of effect size and estimate uncertainty, many species were predicted to occur more often in burned areas, at locations characterized by lower density forest, larger tree size classes, and lower fir or pine canopy cover. Early successional forests were predicted to have higher rates of occupancy for many species. Among mature forests, those with more open structures appear to accommodate more species at higher rates of occupancy. Wildfire and management actions that reduce "clutter" (stand density) are likely to improve foraging habitat quality, especially for fast-flying species adapted to open habitats. When dense, unburned forests are altered through natural disturbance or management, a reduction in clutter, balanced by maintenance of large trees and snags used as roosting sites, would likely benefit many species. Likewise, reforestation efforts that aim to produce relatively open stands dominated by large trees within a heterogeneous landscape, as opposed to homogenous forests characterized by dense stands and closed canopies, would more likely accommodate the range of habitats needed by the Sierran bat community.

Introduction

Wildfire is an important ecological process that drives habitat pattern and structure in western forests, and subsequently influences the wildlife species that inhabit them (Buchalski et al. 2013; Campos et al. 2017; Fogg et al. 2017; Steel and Safford 2017; van Mantegm et al. 2015). For bat species, montane forest ecosystems provide foraging, roosting, and hibernating habitat (Lacki et al. 2007). For example, of the 17 bat species in the Sierra Nevada, 13 are known to use trees for roosting at some point in their lifecycle (Lacki et al. 2007); habitat features that are directly affected by wildfire, and forest management. The conifer forests of the Sierra Nevada in particular are adapted to relatively frequent fires dominated by low to moderate burn severities (Agee 1993; Mallek et al. 2013), which help maintain a diversity of forest densities and habitat types (Coppoletta et al. 2016). However, over the past century much of the region has been managed under a policy of fire suppression (Calkin et al. 2005; Sugihara et al. 2006), which has led to myriad changes in Sierra Nevada ecosystems, such as forest densification and loss of landscape heterogeneity. Due to increased tree density, and with the backdrop of a warming climate and longer fire seasons (Westerling 2016; Westerling et al. 2006), when fires ultimately escape suppression efforts they burn with increasingly high-severity (Miller and Safford 2012), and create larger and more homogenous habitat patches (Steel et al. In Press).

In addition to affecting fire patterns, climate change is expected to increase the frequency of extreme weather events that can further affect bat demography directly (O'Shea et al. 2016). Drought events in particular can affect bat populations through direct mortality of individuals and indirectly through alterations of landscape heterogeneity and habitat quality. The recent and prolonged drought in California led to extensive bark beetle infestation and conifers die-off throughout much of the Sierra Nevada Mountains (Young et al. 2017), altering forest habitats and potentially further increasing the risk of large and severe wildfires (Harvey et al. 2014; Stephens et al. 2018).

Bats are a diverse and functionally important part of the wildlife community in Sierra Nevada forests. The species found in the Sierra Nevada feed nearly exclusively on insects, and consume large amounts of insect biomass every night (Brigham 2010). In some agricultural systems bats provide an ecosystem service in the form of pest-reduction with significant economic value (Boyles et al. 2011). Bats may suppress pest outbreaks in forest systems as well, but the magnitude of this effect has yet to be evaluated. Bats face a number of threats including destruction of habitat, altered disturbance regimes, climate change, and the spread of white-nosed syndrome across the United States (Frick et al. 2016; Lacki et al. 2007).

Despite their prominent place among the diversity and ecology of western forests, and the growing threats to bat populations nation-wide, the community is relatively under-studied (Miller et al. 2003). The relative lack of research into bats as a class of wildlife is in part due to the difficulty of monitoring bat occurrence and habitat use. Surveys of roosting and breeding colonies (e.g., caves and bridges), as well as mist net captures of individuals, have been the primary methods of monitoring bat species for many years (Lacki et al. 2010). Such methods provide valuable and detailed information about the health and reproduction of a select number of individuals and species, but the ability to monitor across the range of habitats used by bats is limited. Furthermore, colony surveys and mist-netting can be costly in terms of surveyor effort. In recent years, as technology has improved, the use of automated recording units (ARUs) have grown in prominence as a complimentary survey technique (Frick 2013). ARUs record the echolocation calls of foraging and commuting bats, which can be later classified to species using associated software. ARUs can be deployed for weeks at a time and conduct nightly surveys with only periodic effort by field technicians.

Among the areas where our understanding of bat ecology is particularly limited is their response to fire-altered habitats and post-fire forest management (but see Buchalski et al. 2013). Understanding how the range of fire effects influence bat occurrence and activity is essential for predicting how wildfires affect species of concern. Large wildfire areas in the Sierra Nevada are priorities for management, especially areas with a high proportion of high-severity burn, due to concerns regarding sustaining forest cover, mitigating future fire risk, and maintaining habitat for wildlife communities. Where reforestation efforts are implemented, standing dead trees are often removed within one to two years post-fire, followed by shrub abatement efforts and planting of desired tree species (typically pines). Studies assessing the influence of salvage logging on the wildlife community have shown mixed effects (Cahall and Hayes 2009; Kotlier et al. 2002). One notable finding among these studies is that lower abundance of snags reduces nesting habitat and rates of occurrence of cavity nesting bird species in the years immediately following the fire (Hutto and Gallo 2006; Saab et al. 2009). Salvage logging may similarly result in a loss of roosting habitat for cavity roosting bat species. Importantly, previous studies have also found that forest management that reduces forest density and foraging "clutter" can lead to increases and bat activity levels for some species (Bender et al. 2015; Hayes and Loeb 2010; Johnson and Chambers 2017). Large burns such as the Power, Chips, and Rim fires are becoming more common in the Sierra Nevada and throughout much of the West, and monitoring their effects on the bat and other wildlife communities is crucial for informing ongoing post-fire management as well as future efforts in burned areas.

Methods

Study design & sampling protocol

The study areas includes the 2004 Power Fire, the 2012 Chips Fire (including reburn areas with the 2000 Storrie Fire), and the 2013 Rim Fire. Respectively, these fires encompassed approximately 6,900 ha, 31,100 ha, and 104,500 ha, of which 38%, 22%, and 36% burned at high-severity. Acoustic bat surveys were conducted May–September of 2014–2017 within these burned areas as well as in the surrounding unburned yellow pine and mixed conifer forests, located on the Eldorado, Plumas, Lassen, and Stanislaus National Forests (Figure 1). Survey locations were selected to sample the range of burn survey and post-fire management actions within these fires as well as nearby unburned forests as reference. Complete descriptions of site selection can be found in Steel and Safford (2017) and Campos et al. (2017).
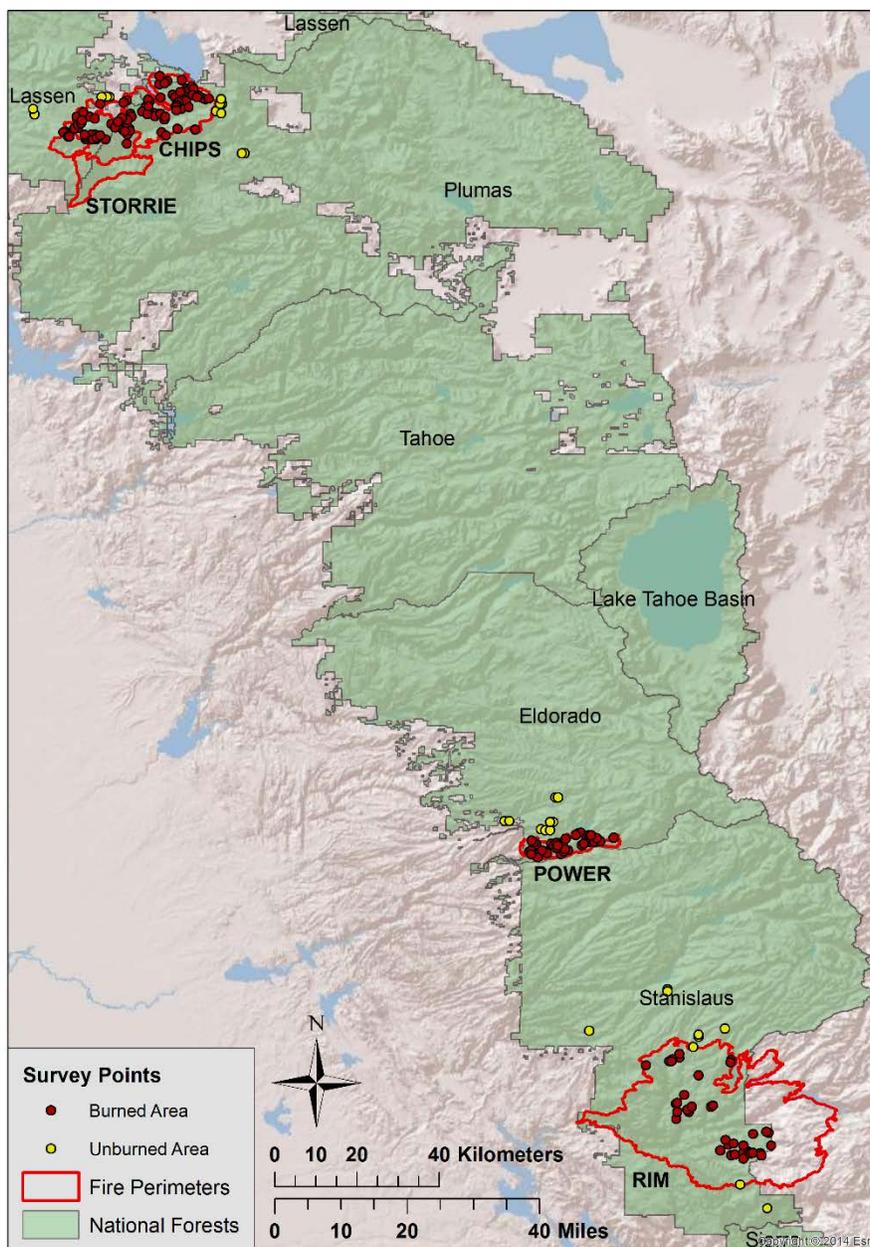
Figure 1. Bat monitoring study region. The three burned areas are shown along with survey locations within and around them.

Bat surveys were conducted using automated recording units (ARUs; SM3BAT model - Wildlife Acoustics Inc.) coupled with ultrasonic microphones (SMM-U1 model - Wildlife Acoustics Inc.). ARUs were deployed for approximately two weeks at a time (equal to the estimated life of internal batteries), recording bats during alternate nights[1] from 30 minutes prior to sunset to 30 minutes following sunrise. During 2017 surveys of the Power fire, recordings were conducted every night, which resulted in more survey nights per deployment. Rare equipment failures and variable battery life resulted in some

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[1] Owl calls were recorded using a non-ultrasonic microphone during alternate nights (results not reported here).

deployments with few survey nights in all years. Battery life depends on a number of factors including the amount of bat activity and false acoustic triggers, as well as the type of batteries used. Most deployments used internal D batteries, but for two of the fires surveyed (Power and Rim) one unit per survey period was coupled with a higher capacity external 12-volt battery that allowed for additional survey nights. Consequently the number of successful survey nights per deployment ranged from 1 to 21 nights with a mean of 6.3 nights. In total, 331 unique locations and 2091 survey nights were sampled over the four years, with many locations resampled in multiple years (Table 1).

Table 1. Acoustic monitoring effort for 2014-2017 across three burned areas and surrounding unburned forest.

Sample Area	Survey Years	Locations	Survey Nights
Power fire	2014-2017	96	714
Chips/Storrie fires	2015-2016	104	535
Rim fire	2014-2016	69	418
Unburned forest*	2014-2017	62	424
All		331	2091

* Includes points in Lassen, Plumas, Eldorado and Stanislaus National Forests

For each survey period, ARUs were secured to vegetation at a survey location (usually a tree or snag) using a chain and combination lock. Ultrasonic microphones were attached to the ARU via a cable and elevated approximately 3m above the ground using a pole supported by vegetation or a piece of rebar. Microphones were located away from branches, other sources of clutter, and sound-reflective surfaces that might distort acoustic recordings. Microphones were pointed toward open areas (relative to the habitat being sampled) to maximize the likelihood of detecting a passing bat (Figure 2).

Figure 2. Example automated recording unit and microphone setup.

Processing protocol

Each recorded bat pass was classified using Sonobat version 3.2.1 with the US west license (Szewczak 2010). The software classifies recordings to species when possible and to broader taxonomic groups (e.g. high- vs. low-frequency species) when recording quality is poor or when discrimination between similar species is inconclusive. Classifications are made by comparing call characteristics of recorded bat passes against a library of known bat calls for 17 California bat species (Table 2; Figure 3). Sonobat also assigns a likelihood of presence for each species during a given night and provides a nightly corrected count of each species. Corrected counts are a conservative estimate of the number of recordings for each species as many low quality or ambiguous recordings are not counted. The automated classification process is intentionally conservative to reduce the likelihood of problematic false presences, but by doing so increases the rate of less problematic false absences, which can be accounted for statistically. In some

cases subsequent manual review of recordings can confirm presence of a species when the software classifications are equivocal. We conducted complete manual reviews for the three National Forest sensitive species in order to reduce the rates of false absences (Table 2).

Table 2. The common name, scientific name and species code of 17 species known to occur in the Sierra Nevada, ordered alphabetically by common name.

Common Name	Scientific Name	Species Code
Big brown bat	*Eptesicus fuscus*	epfu
California myotis	*Myotis californicus*	myca
Fringed myotis*	*Myotis thysanodes*	myth
Hoary bat	*Lasiurus cinereus*	laci
Little brown bat	*Myotis lucifugus*	mylu
Long-eared myotis	*Myotis evotis*	myev
Long-legged myotis[†]	*Myotis volans*	myvo
Mexican free-tailed bat[†]	*Tadarida brasiliensis*	tabr
Pallid bat*	*Antrozous pallidus*	anpa
Silver-haired bat	*Lasionycteris noctivagans*	lano
Small-footed myotis	*Myotis ciliolabrum*	myci
Spotted bat[†]	*Euderma maculatum*	euma
Townsend's big-eared bat*[†]	*Corynorhinus townsendii*	coto
Western mastiff bat[†]	*Eumops perotis*	eupe
Western pipistrelle	*Parastrellus hesperus*	pahe
Western red bat	*Lasiurus blossevillii*	labl

* National Forest sensitive species.
[†] Species for which occupancy models were not fit either due to too few detections or too few non-detections.
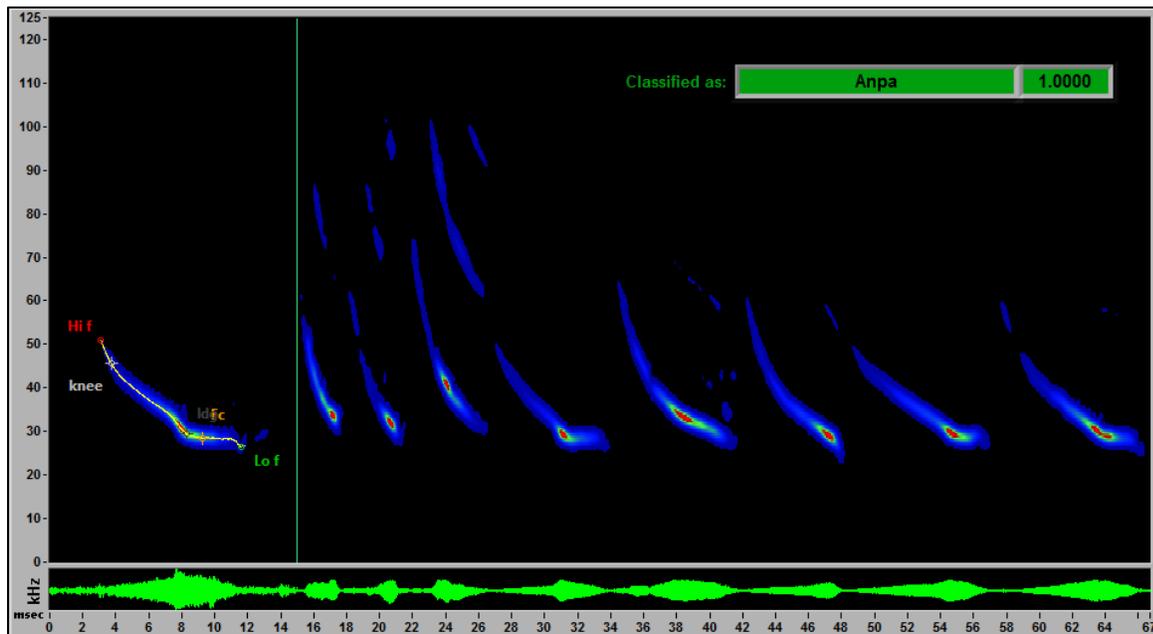

Figure 3. Example sonogram from SonoBat software of a bat call classified as a pallid bat (*Antrozous pallidus*; left) compared to a range of known call types by the same species (right).

Statistical Analysis

In addition to challenges in classification among recorded passes, a species may be present but not detected at all. For example, pallid bat often hunts using auditory cues to find its prey without emitting echolocation calls (Reid 2006). Similarly, the echolocation calls of Townsend's big-eared bats are relatively quiet (Lacki et al. 2010), which means individuals must fly closer to microphones than other species to be detected. Imperfect detection is a common problem when surveying mobile and inconspicuous wildlife. Here we employ occupancy models to explicitly estimate detection probabilities when a species is present and provide unbiased estimates of occurrence rates and effects of environmental covariates of interest (MacKenzie et al. 2003).

We fit two types of occupancy models for as many of the Sierra Nevada bat species as possible: landscape-level models and stand-level models. The aim of the landscape-level models was to build a spatially explicit predictive tool for post-fire footprints in our study region. The stand-level models are intended to assess how individual species respond to the range of habitat structures represented in the yellow-pine and mixed-conifer zones in the central and northern Sierra Nevada. Manipulation of forest structure is the goal of many forest management actions, and these models can help improve our understanding of how such actions may affect bat species.

Models were built using the R statistical environment (R Development Core Team 2017) and the unmarked package (Fiske and Chandler 2011). To identify the best predictive model for each species we compared candidate models using the area under the curve (AUC) statistic. AUC is a measure of model goodness of fit where values close to 1 indicate a model consistently identifies true presences (here true detections) whereas values near 0.5 indicate model predictions are no better than random (Fawcett 2006). Due to imperfect detection occupancy cannot be observed directly. Thus, in order to calculated AUC values we compared model estimates of naïve occupancy (i.e. uncorrected for rates of detection) against observed presence/non-detections.

We used a two-stage model selection process to identify the predictor variables and spatial scales most relevant to bat occupancy:

1) For each species, a near-global model was fit with all single-scale predictors (e.g. temperature max) and one multiple-scale predictor (density, size, and distance) at a time (Table 3). For each varying-scale predictor, a 5-fold cross-validation procedure was conducted to calculate mean AUC values[2]. The scale of each multiple-scale predictor that produced the highest mean AUC of these models was used in the second phase of the model selection process.

2) The following global models were considered in the second stage of model selection with a set of fixed and candidate variables for each landscape- and stand-level model:

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[2] Cross-validation is a procedure where part of the data (in this case 1/5th) is held out of the modeling building processes to be used as testing data in order to generate a fit statistic (e.g. AUC). This is repeated with different subsets of the data (e.g. 5) to generate a mean fit statistic.

Landscape-level model

$$logit(\psi_i) = \beta_{for} * forest_i +$$

$$(\beta_{burn} + \beta_{old} * OldBurn_i + \beta_{sal} * salvage_i + \beta_{sev} * severity_i) * burn_i +$$

$$\beta_{distw} * DistWater_i + \beta_{mtmp} * MaxTemp_i + \beta_{solrad} * SolRad +$$

$$\beta_{dens} * density_i + \beta_{size} * size_i$$

where β_{for}, β_{burn}, and β_{sev} are parameters estimated for fixed variables, and β_{old}, β_{sal}, β_{distw}, β_{mtmp}, β_{solrad}, β_{dens}, and β_{size} represent parameters for candidate variables. For each species, models were fit using all combinations of candidate variables. Each candidate model included all fixed variables. Parameters for old burn/recent burn (i.e. Power vs. Chips and Rim), salvaged/not salvaged, and severity were estimated using data for burned points only (i.e. when $burn_i = 1$). Site was indexed by i. Selection between models of different combinations of candidate variables was done using mean AUC calculated from 5-fold cross-validation, resulting in a final best predictive model for each species.

Stand-level model

$$logit(\psi_i) = \beta_{for} * forest_i +$$

$$\beta_{SnagBA} * SnagBA_i + \beta_{LiveDBH} * LiveBA_i + \beta_{PineCov} * PineCov_i + \beta_{FirCov} * FirCov_i$$

$$+ \beta_{distw} * DistWater_i + \beta_{mtmp} * MaxTemp_i + \beta_{solrad} * SolRad_i$$

where β_{for}, is the parameter for the sole fixed variables (i.e. included in all possible models), and β_{SnagBA}, β_{LiveBA}, $\beta_{PineCov}$, β_{FirCov}, β_{distw}, β_{mtmp}, and β_{solrad} represent parameters for candidate variables. i is the index of site. Selection between models of different combination of candidate variables was done using mean AUC calculated from 5-fold cross-validation, resulting in a final "best" model for each species.

All occupancy models were fit with the following detection model to estimate rates of false absences:

$$logit(p_{ij}) = \alpha_0 + \alpha_{length} * length_{ij} + \alpha_{jday} * jday_{ij} + \alpha_{cc} * cancov_i$$

Length and jday are the survey length in hours and julian day for each site i and survey night j, and cancov is the percent canopy cover within 15m of the bat detector at each site i.

Table 3. Environmental variables used to develop stand-level and landscape-level occupancy models. Local, middle, and landscape scales were calculated at 50 m, 500 m, and 2 km radii, respectively.

Variable (abbrev.)	Description	Scale
Both plot-level and landscape-level models		
National forest (plas, enf, snf)	Three-level categorical variable indicating whether the survey location was within the Plumas/Lassen NFs, Eldorado NF or Stanislaus NF	NA
Survey length (length)	Hours of recording during a survey night	NA
Julian Day (day)	Julian day of the year	NA
Canopy cover (canopy)	Percent canopy cover around the ARU	15 m radius
Distance to water (distance)	Meters to the nearest perennial or intermittent stream, river, or waterbody	intermittent, perennial
Temperature (max temp)	Mean daily maximum temperature (1981-2010)	270 m pixel
Solar radiation (sol rad)	Total annual solar energy exposure (watt-hours / m^2)	30 m pixel
Plot-level models only		
Fir cover	Percent canopy cover of fir species	50 m radius
Pine cover	Percent canopy cover of pine species	50 m radius
Live basal area	Square meters per hectare for live trees	50 m radius
Snag basal area	Square meters per hectare for dead trees	50 m radius
Shrub cover	Percent shrub cover	50 m radius
Landscape-level models only		
Density class (density)	Percent area composed of CWHR[2] density class D (dense forest)	local, middle, landscape
Size class (size)	Percent area composed of CWHR[2] size classes 5 & 6 (medium or large, and multi-layered trees)	local, middle, landscape
Burned (burned)	Boolean indicator of whether a survey location was within a burned area	NA
Old fire (old fire)	Boolean indicator of whether the burn is "old" (i.e. 10-13 years post-fire; input value of one) vs. recent (i.e. 1-4 years post-fire; input value of zero)	NA
Salvaged (salvaged)	Boolean indicator of whether a location was previously salvage logged	NA

[1]RdNBR data were obtained from the US Forest Service Region 5 Remote Sensing Lab and represented the data from the image classified as the "best assessment" of the initial and extended post-fire burn severity assessments.

[2]California Wildlife Habitat Relationships data from US Forest Service Existing Vegetation data.

Forest structure Scenarios

We utilized the final stand-level models to predict the probability of occupancy of each bat species across four forest-structure scenarios. The four scenarios are intended to represent two contrasting mature forest states and two post-fire early successional forest states, each of which represents a different hypothetical result of burn severity and forest management. S1) Mature closed forest – represents a dense second-growth mixed conifer forest, which has not experienced wildfire or active management in many decades. S2) Mature open forest – a second-growth forest, with lower canopy cover but larger fire-resistant trees. This scenario could be a result of low-moderate severity fire and/or active management intended to more closely align with open forests typical of the region's natural range of variation (Safford and Stevens 2017). S3) Early managed – an actively managed plantation one decade following high-severity fire. This scenario could be a result of post-fire salvage logging, shrub abatement and planting of desired conifer species. S4) Early unmanaged – a stand one decade following high-severity fire, which has not experienced active reforestation. To provide a clear contrast with scenario 3, we assume little natural regeneration and a dominant shrub community. Table 4 defines how each scenario is parameterized in order to make bat occupancy predictions using our stand-level models, and Figure 4 provides photo examples of survey sites that approximate each forest condition. Each of the four scenarios are intended to provide examples that span a range of forest conditions which may result from different management goals and strategies. Given the many environmental factors characterizing Sierra Nevada forests, and the variety of management actions and their combinations that can be taken, most actual forest stands will fall somewhere in between such hypotheticals.

Table 4. Forest structure scenarios, their description, and parameterization.

| Forest Structure Scenario	Description	Live basal area	Snag basal area	Shrub cover (%)	Fir cover (%)	Pine cover (%)	Total tree cover (%)
S1: Mature closed forest	A dense second-growth stand, which has experience no active management or wildfire in many decades	60	3	2	50	20	70
S2: Mature open forest	An open "park-like" stand characterized by large fire-resistant trees. Potentially resulting from frequent low-moderate severity fire regime and/or a combination of thinning and Rx burns	60	8	20	10	20	30
S3: Early Managed - 10 years post-fire	Early stages of active reforestation following high-severity wildfire. Resulting from post-fire salvage logging, shrub abatement and planting of desired tree species	5	0	5	5	10	15
S4: Early Unmanaged - 10 years post-fire	Montane shrubland following high-severity wildfire. Resulting from no active post-fire management and limited natural regeneration.	0	15	70	0	0	0
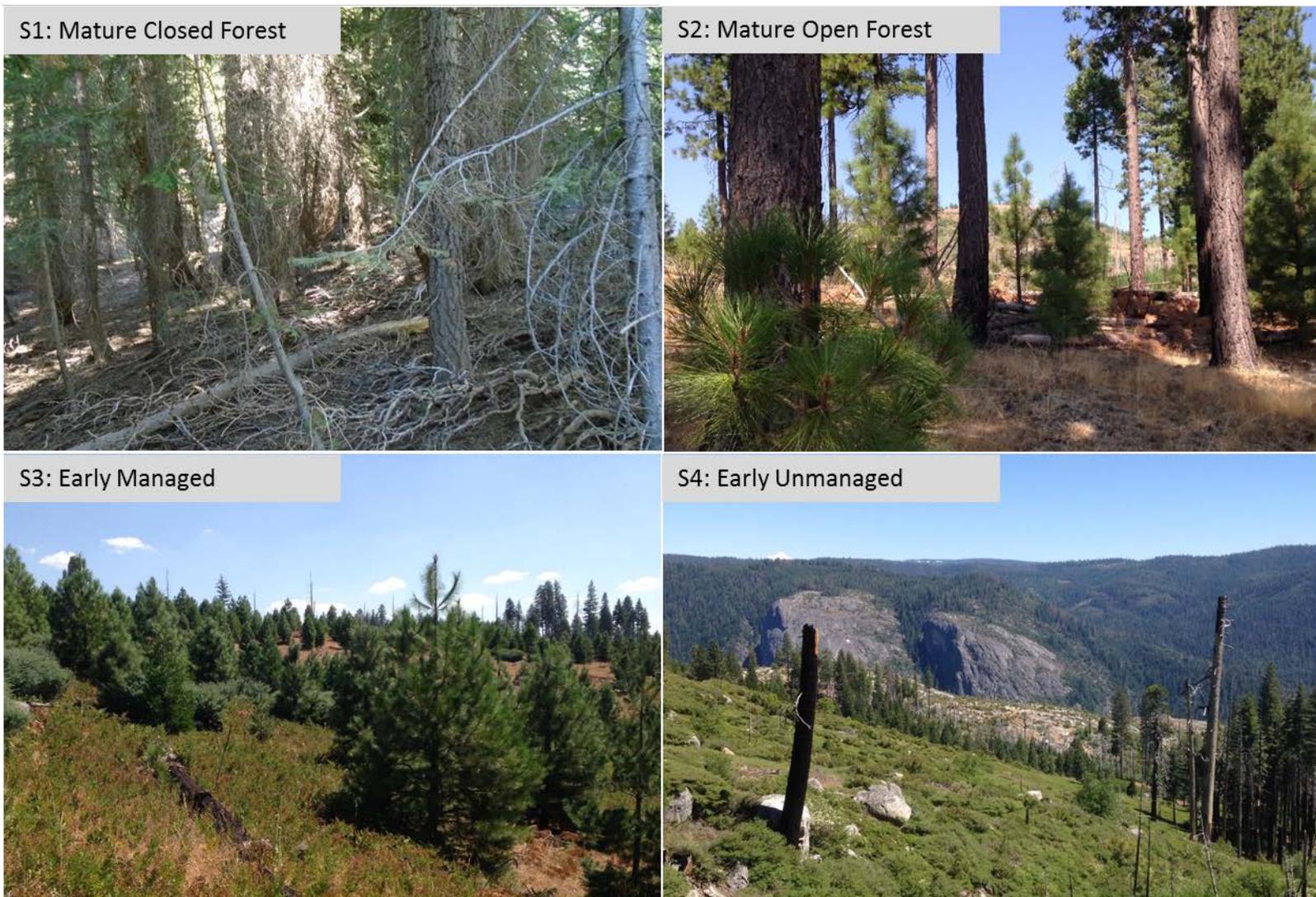
Figure 4. Example images of forest structure scenarios.

Results

Model validation & estimates

We successfully developed occupancy models for 12 Sierra Nevada bat species (Tables 5 & 6). Occupancy models could not be fit for five additional species known to occur in the region either due to insufficient presence data (i.e. rare species) or insufficient absence data (i.e. one near-ubiquitous species; Table 2). The rare species were observed at fewer than 9% of survey locations and include Townsend's big-eared bat (Coto), spotted bat (Euma), western mastiff bat (Eupe), and long-legged myotis (Myvo). Mexican free-tailed bat (Tabr) was observed at 94% of our survey locations. In previous reports using subsets of these data we found that Tabr activity levels were higher in burned areas and with increasing burn severity (Campos et al. 2017; Steel and Safford 2017). Of the 12 species for which we were able to produce occupancy models there was a range of model quality. For three species, the Mackenzie & Bailey test showed poor fit and overdispersion. Mean AUC values ranged from 0.61 to 0.84 (Tables 5 & 6). Landscape-level models with AUC values greater than 0.7 were used to build the accompanying spatial prediction tools (FIRE-BAT; Campos and Steel 2018). Predictive tools were not built for western pipistrelle (Pahe) and long-eared myotis (Myev), which showed significant lack of fit (Table 5). The fringed myotis (Myth) model also showed a lack of fit, but was included due to its importance as a forest sensitive species. Interpretation of FIRE-BAT predictions for Myth as well as forest structure scenario predictions below for Pahe, Myev, and Myth should be made with caution as model uncertainty is likely underestimated.

Table 5. Landscape-level model validation metrics. AUC mean and standard deviations values were calculated using 5-fold cross-validation. Models identified as showing significant lack of fit ($p > 0.05$ and c-hat > 4) are in italics.

| Species | Cross-validation AUC | | Mackenzie & Bailey Test | |
	Mean	Std. Dev.	p-val	c-hat
labl	0.8431	0.0559	0.76	0.03
myca	0.8213	0.1097	0.37	0.94
lano	0.8137	0.0114	0.43	0.48
mylu	0.8048	0.0480	0.43	1.11
pahe	*0.8012*	*0.0361*	*0.00*	*815.52*
myth	*0.7279*	*0.0398*	*0.00*	*20.14*
myev	*0.7198*	*0.0106*	*0.01*	*8.14*
anpa	0.7184	0.0634	0.24	0.91
laci	0.6962	0.0408	0.57	0.90
epfu	0.6649	0.0423	0.69	0.10
myci	0.6527	0.0271	0.09	2.76
myyu	0.6321	0.0839	0.21	0.24

Table 6. Stand-level model validation metrics. AUC mean and standard deviations values were calculated using 5-fold cross-validation. Models identified as showing significant lack of fit (p > 0.05 and c-hat > 4) are in italics.

	Cross-validation AUC		Mackenzie & Bailey Test	
Species	**Mean**	**Std. Dev.**	**p-val**	**c-hat**
labl	0.8350	0.0426	0.77	0.00
lano	0.7970	0.0602	0.35	0.77
pahe	*0.7947*	*0.0435*	*0.00*	*100.90*
mylu	0.7810	0.0555	0.22	1.60
laci	0.7402	0.0436	0.50	0.97
myca	0.7340	0.0808	0.34	0.77
myev	*0.7149*	*0.0349*	*0.00*	*9.79*
myth	*0.7138*	*0.0842*	*0.00*	*16.71*
epfu	0.6721	0.0849	0.67	0.18
myci	0.6647	0.0659	0.11	1.17
anpa	0.6528	0.0586	0.26	0.46
myyu	0.6115	0.0461	0.35	0.46

Standardized parameter estimates for all landscape- and stand-level models are presented graphically in Figures 5 and 6, as well as tabulated in Appendices A and B. For both groups of models, the national forest blocking variable often showed higher effect sizes than other predictors. This suggests that a survey's general location within the region may act as a primary filter as each species' rate of occurrence varies across its distribution. Given a species' general availability in the region, additional model predictors describe local variation in habitat quality as it correlates with more fine-scale environmental factors.

For the landscape-level models, the effect of average maximum temperature, burn severity, distance from water, old fire, and solar radiation varied widely, with no consistent relationships across species. Estimates of the effect of a location being within a burned areas were consistently positive, with 95% confidence intervals completely above zero for California myotis (Myca), and silver-haired bat (Lano). A number of species, especially Pahe, Lano, hoary bat (Laci) and Anpa showed a negative association with dense forests, and Myth, little brown bat (Mylu), Myev, Lano, and Anpa showed a positive relationship with forests characterized by larger size classes. If a location was salvage logged, the probability of occupancy was higher for Myci, and Laci (Figure 5).

Similar to the landscape-level models, within the stand-level models, the effects of average maximum temperature, distance to water, and solar radiation varied across species. Relationships among the percentage of fir and pine cover predictors were most generalizable among species. When these variables were included in the final model, parameter estimates were negative in all cases. 95% confidence intervals did not encompass zero for fir cover in the case of Myth and Laci, and for pine cover in the case of Lano, and Epfu. Myev showed a strong positive relationship with live basal area. The effect of snag basal area was somewhat mixed among species, with Myev again showing a positive relationship, but with Myci, and Laci showing a negative relationship. Percent shrub cover was only included in three of the final models, with an estimated negative effect on Myyu occupancy, and a positive effect on Lano occupancy (Figure 6).

Figure 5. Parameter estimates for landscape-level occupancy models. Mean estimates and 95% confidence intervals are indicated by points and error bars respectively. Values are standardized for comparison of effect sizes. The scale of the x-axis in the first row (blocking effects of National Forest group) differs from the other rows.
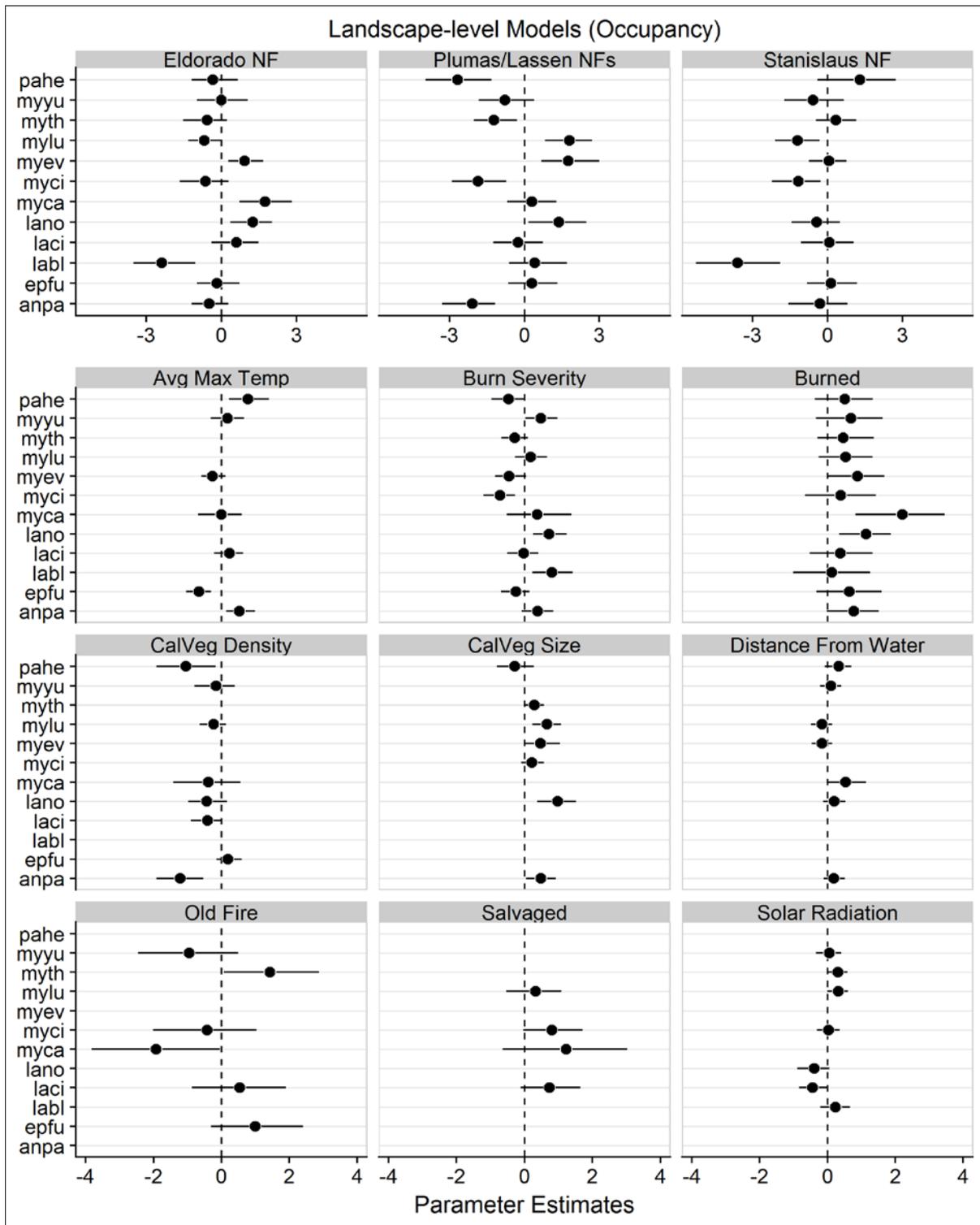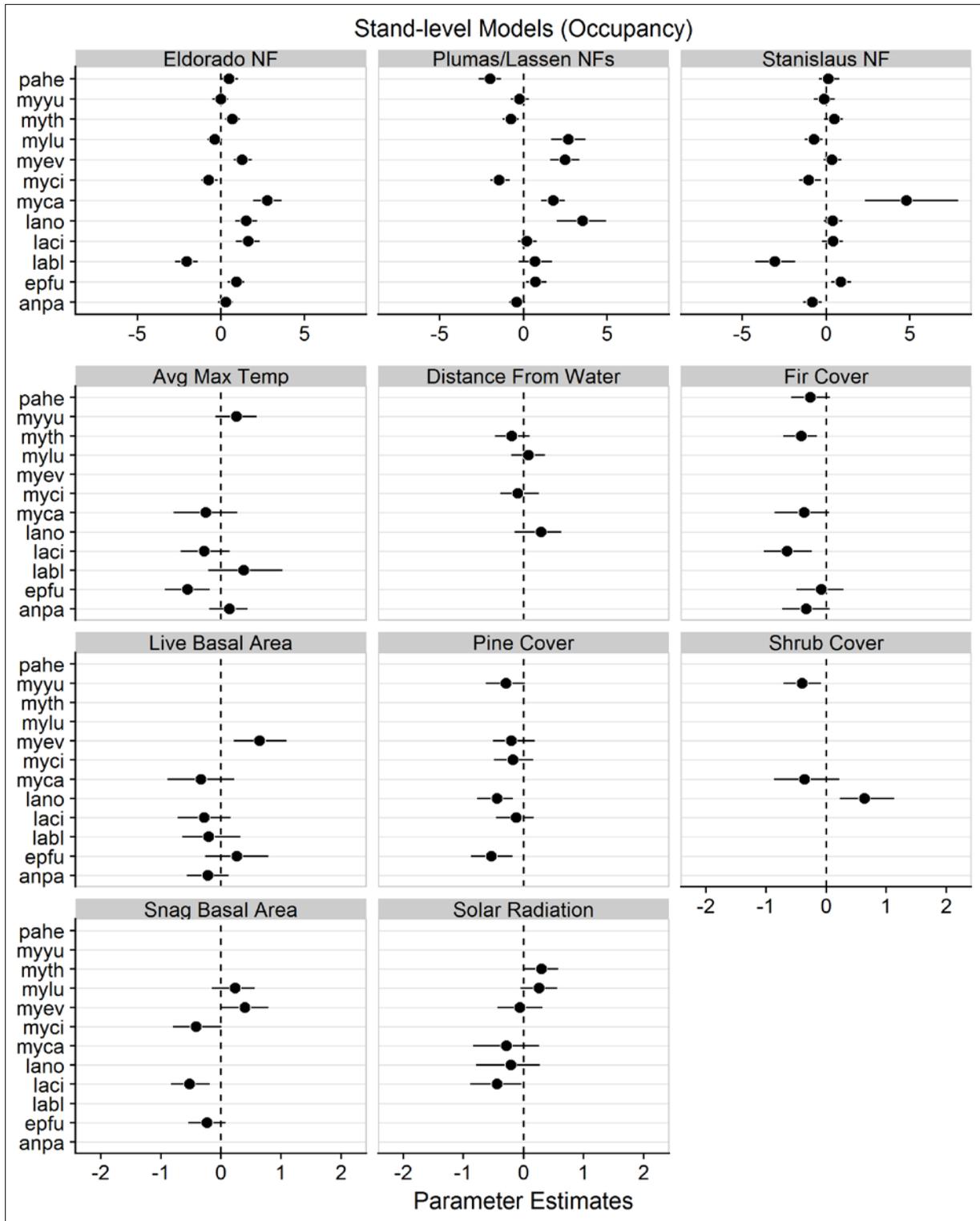
Figure 6. Parameter estimates for stand-level occupancy models. Mean estimates and 95% confidence intervals are indicated by points and error bars respectively. Values are standardized for comparison of effect sizes. The scale of the x-axis in the first row (blocking effects of National Forest group) differs from the other rows.

Parameter estimates for detection covariates were largely consistent between landscape- and stand-level models. Canopy cover was often negatively correlated with the rate of detection, especially for Pahe, Lano, Laci, Labl, and big brown bat (Epfu). The rate of detection increased as the season progressed (with Day) for Pahe, Myev, Myci, Myca, western red bat (Labl), Epfu, and Anpa. The effect of survey length was generally small but predictably positive for Pahe, Myth, Myca, and Laci. Somewhat surprisingly the effect was estimated to be negative for Mylu and Lano (Figure 7). We find it unlikely that detection rates would decline with increased sampling effort. Because survey length varied little between nights within our dataset, these results may be more representative of random noise within the data than a true statistical signal, although additional surveys with a broader range of length would be needed to test such a hypothesis.
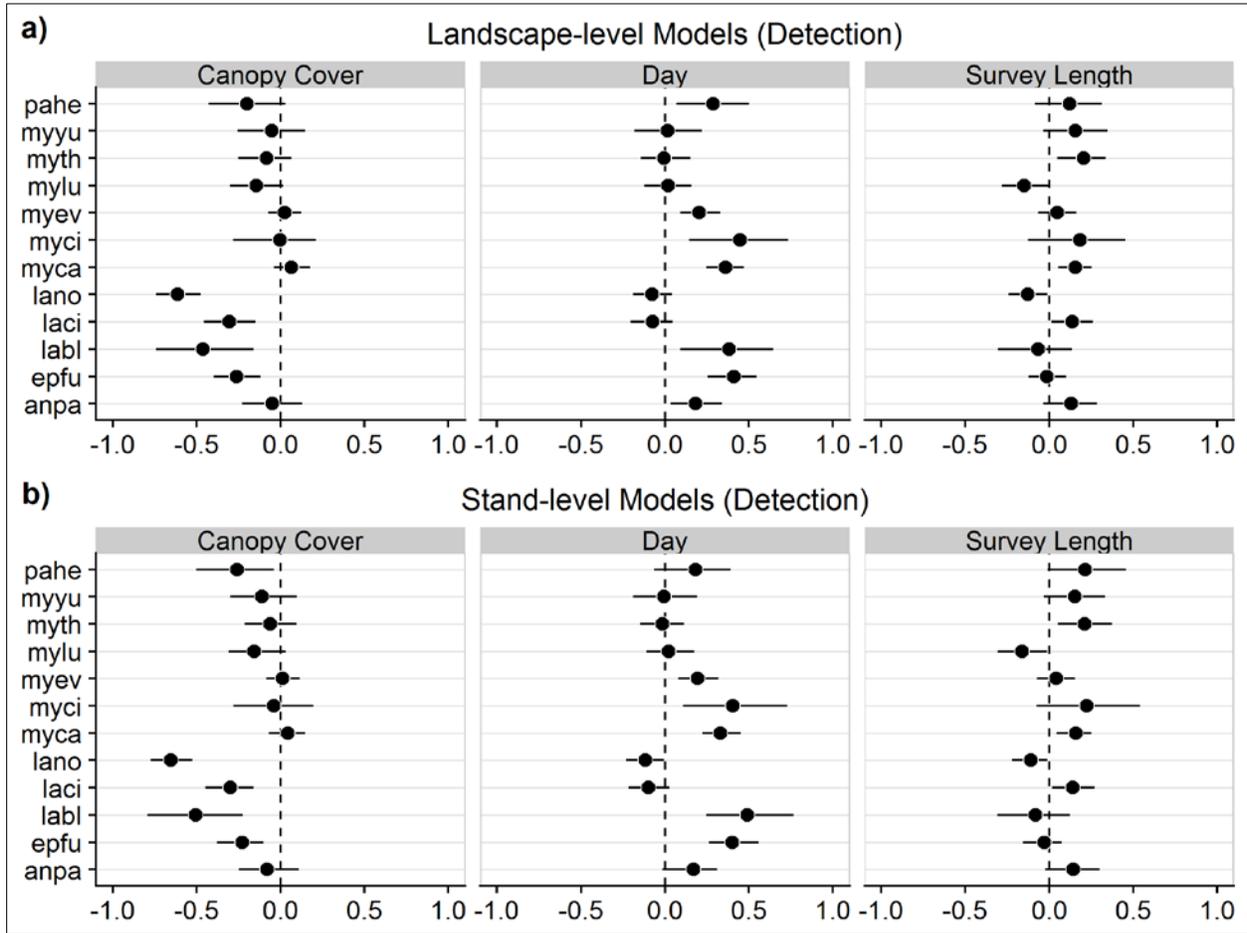
Figure 7. Parameter estimates for a) landscape-level and b) stand-level detection models. Mean estimates and 95% confidence intervals are indicated by points and error bars respectively. Values are standardized for comparison of effect sizes.

Forest structure scenarios

Most species models predicted the highest rates of occupancy in the early successional habitat types, both managed and unmanaged. The mean occupancy rate was slightly higher for the early managed scenario (S3) than for the early unmanaged scenario (S4), but median values were identical between the two. When considering later successional stages, the open forest scenario (S2) often resulted in higher occupancy predictions than the closed forest scenario (S1; Table 7). However, the magnitude of the

differences between scenarios varied greatly among species. For example, the Laci model predicted large differences between scenarios with the species predicted to occur most frequently in early managed stands and least frequently in mature closed forest. Conversely, predictions for Mylu varied little between scenarios. The magnitude of the difference among scenarios was also dependent on national forest group. For example, Myca is predicted to be nearly universally present regardless of habitat type within the Stanislaus National Forest, but occurrence rates are lower and more dependent on forest structure in the Plumas/Lassen National Forests (Figure 8).

Table 7. Mean predicted occupancy rate across the three National Forest groups for each forest structure scenario. For each species, the highest predicted rate among scenarios is in bold. Mean, median and standard deviation of occupancy across species are also listed.

Common Name	Code	S1 - Closed forest	S2 - Open forest	S3 - Early reforestation	S4 - Early unmanaged
western pipistrelle	pahe	0.34	0.43	**0.44**	0.43
Yuma myotis	myyu	0.50	0.43	**0.53**	0.31
fringed myotis	myth	0.38	0.54	**0.56**	0.54
little brown bat	mylu	0.53	0.54	0.52	**0.57**
long-eared myotis	myev	0.91	**0.92**	0.61	0.68
small-footed myotis	myci	0.30	0.27	**0.34**	0.26
California myotis	myca	0.82	0.86	**0.96**	0.90
silver-haired bat	lano	0.69	0.76	0.74	**0.94**
hoary bat	laci	0.34	0.55	**0.82**	0.72
western red bat	labl	0.22	0.22	0.29	**0.30**
big brown bat	epfu	0.77	**0.78**	0.71	0.70
pallid bat	anpa	0.21	0.32	**0.49**	0.48
Mean		0.50	0.55	0.58	0.57
Median		0.44	0.54	0.55	0.55
Standard Deviation		0.24	0.23	0.20	0.23

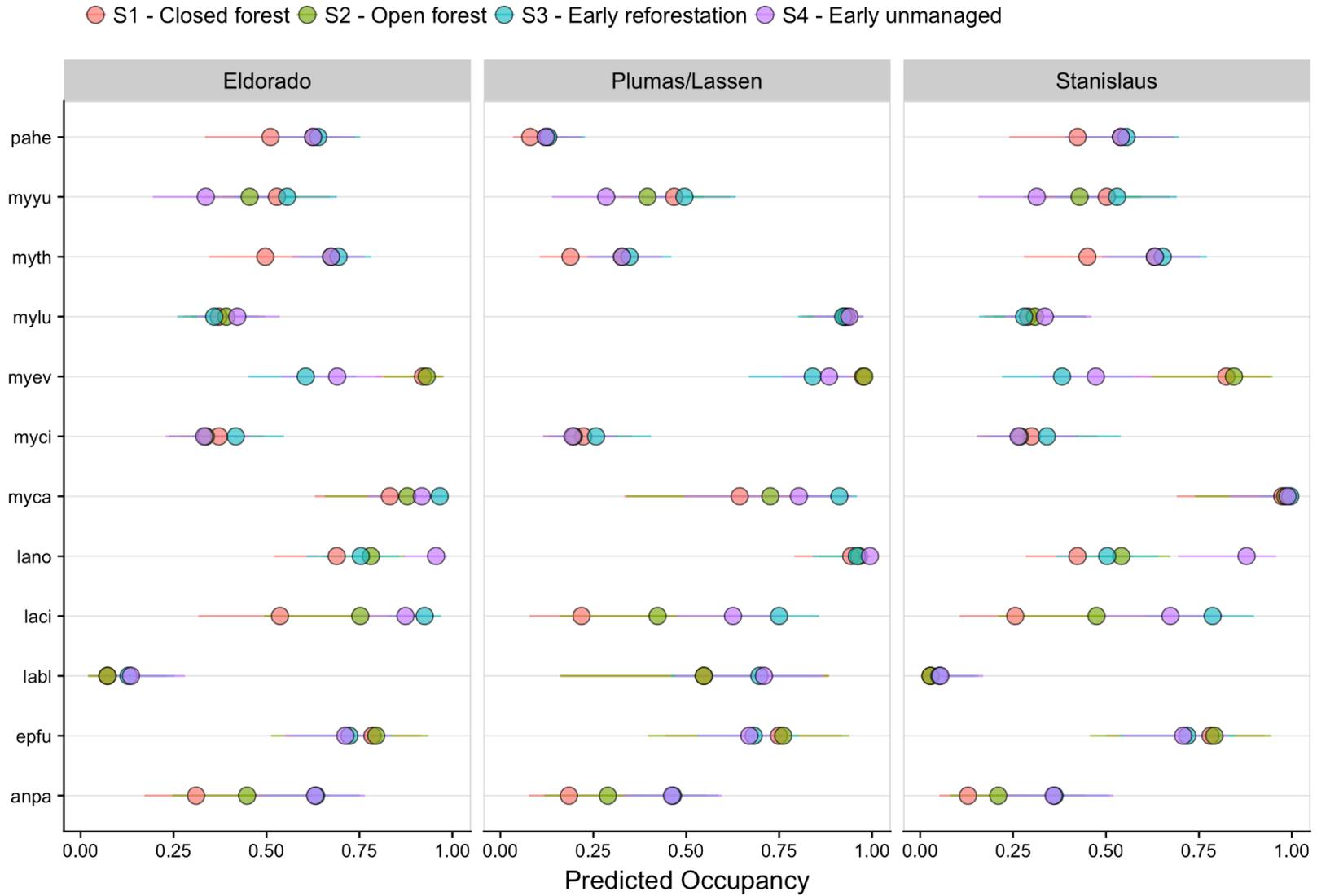**Figure 8.** Predicted occupancy rates for each stand-level species model, forest structure scenario and National Forest group. Mean predictions and 95% prediction intervals are indicated by points and error bars respectively.

Discussion and Management Considerations

Wildfire is a dominant driver of forest pattern and function in the Sierra Nevada (Sugihara et al. 2006), and has profound implications for species diversity, and the geographic distributions for many taxa (Kelly and Brotons 2017; van Mantegm et al. 2015). Important work has been done assessing the impacts of wildfire on some well-studied taxa (i.e. birds and some small mammals; Fontaine and Kennedy 2012), but up to now few studies have focused on bat community associations with burned areas and post-fire forest management (but see Buchalski et al. 2013). Thus, the bat monitoring in and near the Power, Chips/Storrie, and Rim burn areas represents an important opportunity to advance our knowledge of bats in this system, and better inform wildlife and forest management in the region.

The suitability of forest ecosystems for bat species can be characterized by the abundance of roost sites, the amount of clutter, availability of prey, and availability of water (Hayes and Loeb 2010). In this context, clutter is roughly defined as the difficulty of negotiating vegetation structure while foraging, and is related to vegetation density and structural complexity. Wildfire and forest management have the potential to influence the quality of these resources for bats through manipulation of forest vegetation. Much of the published literature are most relevant to how these manipulations affect the availability of roost structures (i.e. in live trees and snags), and foraging habitat quality as related to vegetation clutter (Lacki et al. 2010). Acoustic surveys such as those used here are best able to evaluate foraging rates, and identify effects of forest alterations on foraging habitat quality. Roosting habitat quality can be inferred only indirectly as bats are more likely to forage in areas in close proximity to roosting sites, all else being equal.

Foraging habitat

The findings presented here show many species occur more often in burned areas, habitats characterized by low density forests, low canopy cover, and low basal area of both live and dead trees (Figures 5, 6, & 8). Wildfire, prescribed burns, and mechanical tree removal reduce the clutter of forest environments, potentially improving the ability of some species to forage. Bat species vary in size and wing morphology, characteristics that affect flight speed and maneuverability. Small-bodied bats with low wing-loading (body mass / wing area) are able to hunt relatively effectively in cluttered environments such as dense, closed-canopy forests, while large bats with high wing-loading are observed foraging more often in open forests or clearings (Johnson and Chambers 2017; Lacki et al. 2010). In particular, dense forests which have not experienced wildfire or active management may represent low foraging habitat quality for many species and largely inaccessible to some. This indicates that wildfire is an important ecological process for a bat community adapted to an ecosystem historically characterized by frequent fire and heterogeneous landscapes. Dense forests are currently common in the Sierra Nevada due to a century of fire suppression (Steel et al. 2015), and a shift to more open forest types would likely benefit the forest bat community as a whole. Increasing the use of prescribed burns and managed wildfire in the region would help with such a transition, and would provide other ecological and economic benefits as well (North et al. 2012). Forestry treatments that remove snags or live trees may also increase foraging habitat quality for some species, but often at the detriment to roost availability (Hayes and Loeb 2010).

Roosting habitat

Bats use a variety of structures for roosting in forest ecosystems. These structures include relatively permanent natural features such as rocky outcroppings, cliffs or caves, and human infrastructure such as bridges, buildings or mines. Additionally, 13 of the 17 bat species surveyed, including the three forest service sensitive species, are known to roost in live or dead trees (snags) at some point during their lifecycle. These include the pallid bat, Townsend's big-eared bat, spotted bat, silver-haired bat, western red bat, hoary bat, California myotis, long-eared myotis, fringed myotis, long-legged myotis, and Yuma myotis (Lacki et al. 2007). Some species including hoary bat will roost in the foliage of live trees, while many others will utilize features of snags such as cavities, crevices, exfoliating bark (e.g. California myotis), furrows in the bark (e.g. silver-haired bat), and abandoned woodpecker holes, or defects of living trees (Lacki et al. 2010). Roost trees tend to be tall, large in diameter, and located in stands with an open canopy, high density of snags (Ruppell et al. 2005), and near water and riparian areas (Brigham 2010).

Moderate- and high-severity fire creates high densities of snags, and effectively high densities of potential roosting sites for many species. Therefore, salvage logging operations that remove large-diameter snags may reduce the availability of high quality roosting sites. However, similar to cavity-nesting birds, time since fire and the decay level of snags may influence the suitability of existing snags as roosting habitat (Hayes and Loeb 2010; Saab et al. 2004). Generally, whether a location was salvage logged or not was a poor predictor of species occupancy reported here, and of activity levels assessed in previous reports specific to the Power and Chips fires (Campos et al. 2017; Steel and Safford 2017). Two possible exceptions are hoary bat (Laci) and small-footed myotis (Myci) which showed some evidence of higher rates of occupancy in salvaged areas, and areas with lower snag basal area (Figures 5 & 6). These species primarily roost in foliage of live trees and in rock crevices and caves respectively, so may be benefitting from reduced clutter and improved foraging habitat without a loss in roosting habitat. If salvage logging negatively affects snag roosting bat species, it was not immediately evident from our acoustic surveys, which better sample foraging activity than nesting activity. However, in ponderosa pine forests of New Mexico, a telemetry study found a majority of roosts for two *Myotis* species (including long-eared myotis) occurred in unthinned forests as compared to thinned forests, and that large-diameter snags (>68 cm at breast height) were preferentially selected as roost sites (Johnson and Chambers 2017). This is supported by our findings that long-eared myotis (Myev) is positively associated with live tree and snag basal area, despite the increased clutter (Figures 5 & 6). Management activities promoting the persistence, and future creation of large diameter live trees and snags would likely benefit many forest bat species that utilize trees as roosts (Barclay and Kurta 2010; Hayes and Loeb 2010). In the short term, retention of large trees and snags would help maintain existing roost sites, while the removal of small-diameter trees and understory vegetation through low- and moderate-severity wildfire or active management may improve foraging habitat. Long-term management strategies that promote heterogeneous landscapes with a high proportion of open mature forests rather than dense cluttered forests, would ensure roosting sites are continuously available and foraging habitat remains accessible.

Acknowledgements

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Appendices

Appendix A – Parameter estimates for landscape-level occupancy models

sp	outcome	par	Estimate	SE	lower95	upper95	p_val
anpa	occupancy	dens	-1.21	0.334	-1.833	-0.57	0
anpa	occupancy	dist	0.19	0.154	-0.116	0.462	0.219
anpa	occupancy	size	0.478	0.218	0.062	0.895	0.028
anpa	occupancy	tmx	0.53	0.212	0.112	0.939	0.012
anpa	occupancy	burned	0.769	0.391	-0.052	1.521	0.049
anpa	occupancy	forestenf	-0.497	0.394	-1.222	0.253	0.207
anpa	occupancy	forestplas	-2.082	0.526	-3.008	-0.997	0
anpa	occupancy	forestsnf	-0.311	0.609	-1.461	0.927	0.61
anpa	occupancy	burned:sev	0.389	0.236	-0.037	0.882	0.099
anpa	detection	(Intercept)	-0.823	0.086	-0.999	-0.657	0
anpa	detection	jday	0.183	0.085	0.019	0.335	0.031
anpa	detection	length	0.132	0.082	-0.026	0.296	0.105
anpa	detection	cc	-0.049	0.095	-0.242	0.134	0.606
epfu	occupancy	dens	0.195	0.199	-0.205	0.597	0.328
epfu	occupancy	tmx	-0.659	0.198	-1.069	-0.282	0.001
epfu	occupancy	burned	0.644	0.501	-0.403	1.549	0.198
epfu	occupancy	forestenf	-0.188	0.437	-1.061	0.603	0.667
epfu	occupancy	forestplas	0.297	0.496	-0.625	1.163	0.549
epfu	occupancy	forestsnf	0.139	0.506	-0.752	1.208	0.783
epfu	occupancy	burned:old_fire	1	0.689	-0.355	2.24	0.147
epfu	occupancy	burned:sev	-0.256	0.215	-0.707	0.13	0.234
epfu	detection	(Intercept)	-0.365	0.062	-0.488	-0.251	0
epfu	detection	jday	0.412	0.075	0.26	0.554	0
epfu	detection	length	-0.014	0.058	-0.119	0.1	0.815
epfu	detection	cc	-0.261	0.071	-0.391	-0.121	0
labl	occupancy	solrad	0.238	0.229	-0.172	0.664	0.297
labl	occupancy	burned	0.129	0.571	-0.931	1.247	0.822
labl	occupancy	forestenf	-2.38	0.625	-3.629	-1.125	0
labl	occupancy	forestplas	0.419	0.583	-0.783	1.512	0.472
labl	occupancy	forestsnf	-3.605	0.842	-5.131	-1.779	0
labl	occupancy	burned:sev	0.802	0.312	0.187	1.382	0.01
labl	detection	(Intercept)	-1.398	0.152	-1.678	-1.106	0
labl	detection	jday	0.382	0.141	0.12	0.647	0.007
labl	detection	length	-0.067	0.116	-0.287	0.15	0.564
labl	detection	cc	-0.461	0.152	-0.746	-0.15	0.002
laci	occupancy	dens	-0.414	0.26	-0.899	0.11	0.112
laci	occupancy	solrad	-0.442	0.215	-0.836	-0.006	0.04

laci	occupancy	tmx	0.245	0.223	-0.159	0.76	0.27
laci	occupancy	burned	0.378	0.462	-0.495	1.215	0.414
laci	occupancy	forestenf	0.598	0.489	-0.36	1.491	0.221
laci	occupancy	forestplas	-0.265	0.521	-1.203	0.76	0.611
laci	occupancy	forestsnf	0.08	0.542	-1.021	1.018	0.882
laci	occupancy	burned:old_fire	0.538	0.728	-0.947	1.881	0.46
laci	occupancy	burned:salvage	0.733	0.403	-0.052	1.528	0.069
laci	occupancy	burned:sev	-0.024	0.224	-0.491	0.405	0.914
laci	detection	(Intercept)	-0.598	0.067	-0.72	-0.467	0
laci	detection	jday	-0.073	0.063	-0.191	0.048	0.251
laci	detection	length	0.137	0.067	0.002	0.261	0.04
laci	detection	cc	-0.305	0.077	-0.436	-0.145	0
lano	occupancy	dens	-0.433	0.291	-0.999	0.075	0.137
lano	occupancy	dist	0.203	0.168	-0.12	0.516	0.228
lano	occupancy	size	0.971	0.291	0.459	1.559	0.001
lano	occupancy	solrad	-0.397	0.238	-0.871	0.049	0.096
lano	occupancy	burned	1.138	0.392	0.355	1.872	0.004
lano	occupancy	forestenf	1.258	0.424	0.392	2.103	0.003
lano	occupancy	forestplas	1.379	0.606	0.233	2.739	0.023
lano	occupancy	forestsnf	-0.438	0.513	-1.524	0.513	0.393
lano	occupancy	burned:sev	0.729	0.254	0.239	1.223	0.004
lano	detection	(Intercept)	0.238	0.058	0.119	0.341	0
lano	detection	jday	-0.076	0.059	-0.19	0.039	0.201
lano	detection	length	-0.128	0.058	-0.235	-0.018	0.029
lano	detection	cc	-0.613	0.068	-0.746	-0.488	0
myca	occupancy	dens	-0.383	0.527	-1.361	0.696	0.468
myca	occupancy	dist	0.532	0.283	-0.06	1.039	0.06
myca	occupancy	tmx	-0.005	0.323	-0.644	0.575	0.988
myca	occupancy	burned	2.199	0.691	0.843	3.427	0.001
myca	occupancy	forestenf	1.745	0.567	0.691	2.864	0.002
myca	occupancy	forestplas	0.293	0.528	-0.771	1.291	0.579
myca	occupancy	burned:old_fire	-1.929	0.99	-3.795	0.009	0.051
myca	occupancy	burned:salvage	1.23	0.911	-0.693	2.858	0.177
myca	occupancy	burned:sev	0.374	0.485	-0.529	1.411	0.441
myca	detection	(Intercept)	0.985	0.053	0.874	1.077	0
myca	detection	jday	0.361	0.056	0.243	0.466	0
myca	detection	length	0.155	0.051	0.052	0.248	0.002
myca	detection	cc	0.064	0.056	-0.057	0.165	0.25
myci	occupancy	size	0.214	0.171	-0.17	0.511	0.212
myci	occupancy	solrad	0.035	0.167	-0.284	0.329	0.831
myci	occupancy	burned	0.387	0.553	-0.558	1.424	0.484
myci	occupancy	forestenf	-0.639	0.503	-1.516	0.396	0.204
myci	occupancy	forestplas	-1.86	0.554	-2.86	-0.703	0.001

myci	occupancy	forestsnf	-1.172	0.526	-2.223	-0.186	0.026
myci	occupancy	burned:old_fire	-0.425	0.773	-1.931	0.994	0.582
myci	occupancy	burned:salvage	0.805	0.441	-0.08	1.651	0.068
myci	occupancy	burned:sev	-0.717	0.248	-1.164	-0.225	0.004
myci	detection	(Intercept)	-1.26	0.141	-1.531	-1.009	0
myci	detection	jday	0.447	0.157	0.139	0.758	0.004
myci	detection	length	0.183	0.155	-0.099	0.463	0.238
myci	detection	cc	-0.004	0.126	-0.255	0.243	0.972
myev	occupancy	dist	-0.162	0.151	-0.439	0.138	0.281
myev	occupancy	size	0.473	0.264	-0.034	0.952	0.073
myev	occupancy	tmx	-0.261	0.185	-0.657	0.068	0.157
myev	occupancy	burned	0.885	0.413	-0.015	1.656	0.032
myev	occupancy	forestenf	0.93	0.377	0.216	1.624	0.014
myev	occupancy	forestplas	1.748	0.574	0.556	2.814	0.002
myev	occupancy	forestsnf	0.05	0.39	-0.707	0.808	0.897
myev	occupancy	burned:sev	-0.449	0.239	-0.909	0.006	0.06
myev	detection	(Intercept)	-0.188	0.054	-0.287	-0.084	0
myev	detection	jday	0.204	0.059	0.098	0.313	0.001
myev	detection	length	0.049	0.056	-0.063	0.161	0.379
myev	detection	cc	0.026	0.053	-0.081	0.12	0.616
mylu	occupancy	dens	-0.233	0.2	-0.632	0.108	0.243
mylu	occupancy	dist	-0.158	0.158	-0.489	0.14	0.32
mylu	occupancy	size	0.663	0.221	0.3	1.13	0.003
mylu	occupancy	solrad	0.317	0.168	0.01	0.664	0.059
mylu	occupancy	burned	0.538	0.397	-0.258	1.245	0.175
mylu	occupancy	forestenf	-0.694	0.368	-1.427	0.011	0.059
mylu	occupancy	forestplas	1.797	0.493	0.763	2.683	0
mylu	occupancy	forestsnf	-1.206	0.472	-2.122	-0.308	0.011
mylu	occupancy	burned:salvage	0.322	0.4	-0.417	1.119	0.421
mylu	occupancy	burned:sev	0.18	0.241	-0.301	0.673	0.454
mylu	detection	(Intercept)	-0.184	0.066	-0.323	-0.065	0.005
mylu	detection	jday	0.018	0.071	-0.125	0.144	0.798
mylu	detection	length	-0.15	0.073	-0.292	-0.017	0.038
mylu	detection	cc	-0.144	0.085	-0.305	0.009	0.088
myth	occupancy	size	0.285	0.155	-0.006	0.614	0.066
myth	occupancy	solrad	0.309	0.151	0.013	0.585	0.04
myth	occupancy	burned	0.463	0.444	-0.351	1.374	0.297
myth	occupancy	forestenf	-0.57	0.454	-1.482	0.301	0.209
myth	occupancy	forestplas	-1.226	0.44	-2.151	-0.447	0.005
myth	occupancy	forestsnf	0.329	0.431	-0.334	1.273	0.444
myth	occupancy	burned:old_fire	1.425	0.689	0.193	2.796	0.039
myth	occupancy	burned:sev	-0.288	0.2	-0.665	0.077	0.151
myth	detection	(Intercept)	-0.615	0.073	-0.757	-0.468	0

myth	detection	jday	-0.006	0.071	-0.147	0.128	0.933
myth	detection	length	0.205	0.082	0.048	0.364	0.012
myth	detection	cc	-0.084	0.08	-0.239	0.074	0.295
myyu	occupancy	dens	-0.16	0.304	-0.747	0.416	0.599
myyu	occupancy	dist	0.097	0.162	-0.239	0.39	0.551
myyu	occupancy	solrad	0.049	0.182	-0.343	0.366	0.787
myyu	occupancy	tmx	0.183	0.245	-0.359	0.618	0.457
myyu	occupancy	burned	0.685	0.508	-0.274	1.691	0.178
myyu	occupancy	forestenf	0	0.506	-0.951	0.945	1
myyu	occupancy	forestplas	-0.781	0.562	-1.912	0.231	0.164
myyu	occupancy	forestsnf	-0.579	0.61	-1.815	0.596	0.342
myyu	occupancy	burned:old_fire	-0.953	0.754	-2.5	0.408	0.207
myyu	occupancy	burned:sev	0.486	0.243	0.003	0.939	0.045
myyu	detection	(Intercept)	-1.305	0.102	-1.513	-1.119	0
myyu	detection	jday	0.016	0.102	-0.188	0.216	0.873
myyu	detection	length	0.156	0.101	-0.058	0.357	0.123
myyu	detection	cc	-0.053	0.105	-0.244	0.137	0.613
pahe	occupancy	dens	-1.051	0.437	-1.908	-0.213	0.016
pahe	occupancy	dist	0.331	0.2	-0.031	0.705	0.098
pahe	occupancy	size	-0.286	0.275	-0.887	0.242	0.298
pahe	occupancy	tmx	0.786	0.301	0.148	1.338	0.009
pahe	occupancy	burned	0.514	0.463	-0.314	1.457	0.268
pahe	occupancy	forestenf	-0.344	0.461	-1.237	0.578	0.455
pahe	occupancy	forestplas	-2.68	0.663	-3.948	-1.345	0
pahe	occupancy	forestsnf	1.297	0.811	-0.348	2.813	0.11
pahe	occupancy	burned:sev	-0.47	0.258	-1.038	0.015	0.069
pahe	detection	(Intercept)	-1.287	0.112	-1.491	-1.067	0
pahe	detection	jday	0.286	0.108	0.073	0.498	0.008
pahe	detection	length	0.123	0.101	-0.084	0.311	0.223
pahe	detection	cc	-0.2	0.117	-0.448	0.028	0.087

Appendix B – Parameter estimates for stand-level occupancy models

sp	outcome	par	Estimate	SE	lower95	upper95	p_val
anpa	occupancy	ba_live	-0.215	0.185	-0.567	0.127	0.244
anpa	occupancy	cov_fir	-0.329	0.2	-0.728	0.059	0.101
anpa	occupancy	tmx	0.139	0.162	-0.197	0.442	0.392
anpa	occupancy	forestenf	0.291	0.233	-0.177	0.714	0.213
anpa	occupancy	forestplas	-0.399	0.254	-0.848	0.114	0.116
anpa	occupancy	forestsnf	-0.824	0.295	-1.38	-0.257	0.005
anpa	detection	(Intercept)	-0.814	0.086	-0.989	-0.657	0

anpa	detection	jday	0.171	0.085	0.013	0.346	0.044
anpa	detection	length	0.139	0.082	-0.013	0.306	0.091
anpa	detection	cc	-0.066	0.096	-0.235	0.129	0.491
epfu	occupancy	ba_live	0.266	0.275	-0.262	0.793	0.333
epfu	occupancy	ba_snag	-0.228	0.157	-0.543	0.074	0.147
epfu	occupancy	cov_fir	-0.081	0.212	-0.49	0.29	0.702
epfu	occupancy	cov_pine	-0.533	0.18	-0.874	-0.179	0.003
epfu	occupancy	tmx	-0.558	0.195	-0.934	-0.184	0.004
epfu	occupancy	forestenf	0.916	0.258	0.378	1.392	0
epfu	occupancy	forestplas	0.717	0.293	0.154	1.362	0.014
epfu	occupancy	forestsnf	0.895	0.311	0.311	1.502	0.004
epfu	detection	(Intercept)	-0.37	0.064	-0.505	-0.249	0
epfu	detection	jday	0.384	0.076	0.25	0.546	0
epfu	detection	length	-0.024	0.059	-0.127	0.087	0.689
epfu	detection	cc	-0.23	0.071	-0.382	-0.104	0.001
labl	occupancy	ba_live	-0.203	0.252	-0.641	0.323	0.421
labl	occupancy	tmx	0.377	0.311	-0.211	1.027	0.225
labl	occupancy	forestenf	-2.056	0.366	-2.751	-1.381	0
labl	occupancy	forestplas	0.689	0.534	-0.292	1.714	0.197
labl	occupancy	forestsnf	-3.059	0.624	-4.231	-1.849	0
labl	detection	(Intercept)	-1.4	0.162	-1.731	-1.09	0
labl	detection	jday	0.426	0.147	0.123	0.707	0.004
labl	detection	length	-0.094	0.119	-0.321	0.129	0.428
labl	detection	cc	-0.451	0.154	-0.73	-0.138	0.003
laci	occupancy	ba_live	-0.279	0.23	-0.718	0.162	0.226
laci	occupancy	ba_snag	-0.525	0.167	-0.831	-0.185	0.002
laci	occupancy	cov_fir	-0.649	0.208	-1.036	-0.237	0.002
laci	occupancy	cov_pine	-0.12	0.167	-0.459	0.169	0.474
laci	occupancy	solrad	-0.437	0.223	-0.884	-0.032	0.05
laci	occupancy	tmx	-0.275	0.221	-0.67	0.139	0.214
laci	occupancy	forestenf	1.626	0.367	0.887	2.303	0
laci	occupancy	forestplas	0.204	0.296	-0.339	0.777	0.49
laci	occupancy	forestsnf	0.413	0.317	-0.228	1.003	0.192
laci	detection	(Intercept)	-0.589	0.067	-0.721	-0.465	0
laci	detection	jday	-0.097	0.065	-0.225	0.028	0.135
laci	detection	length	0.142	0.068	0.007	0.28	0.037
laci	detection	cc	-0.288	0.076	-0.418	-0.141	0
lano	occupancy	cov_pine	-0.441	0.156	-0.771	-0.172	0.005
lano	occupancy	dist	0.295	0.203	-0.147	0.634	0.146
lano	occupancy	shrub_cov	0.641	0.223	0.231	1.134	0.004
lano	occupancy	solrad	-0.212	0.27	-0.792	0.275	0.432
lano	occupancy	forestenf	1.502	0.33	0.848	2.156	0
lano	occupancy	forestplas	3.528	0.763	1.979	4.939	0

lano	occupancy	forestsnf	0.397	0.275	-0.144	0.984	0.148
lano	detection	(Intercept)	0.203	0.06	0.093	0.328	0.001
lano	detection	jday	-0.116	0.06	-0.231	0.002	0.054
lano	detection	length	-0.109	0.057	-0.228	-0.004	0.057
lano	detection	cc	-0.654	0.067	-0.79	-0.538	0
myca	occupancy	ba_live	-0.335	0.281	-0.886	0.224	0.234
myca	occupancy	cov_fir	-0.361	0.236	-0.861	0.052	0.125
myca	occupancy	shrub_cov	-0.354	0.282	-0.862	0.218	0.209
myca	occupancy	solrad	-0.285	0.282	-0.837	0.258	0.312
myca	occupancy	tmx	-0.254	0.28	-0.787	0.273	0.365
myca	occupancy	forestenf	2.785	0.442	1.935	3.638	0
myca	occupancy	forestplas	1.779	0.371	1.053	2.473	0
myca	occupancy	forestsnf	4.817	1.43	2.312	7.893	0.001
myca	detection	(Intercept)	0.99	0.055	0.867	1.082	0
myca	detection	jday	0.33	0.058	0.218	0.441	0
myca	detection	length	0.158	0.051	0.062	0.265	0.002
myca	detection	cc	0.046	0.057	-0.064	0.153	0.421
myci	occupancy	ba_snag	-0.413	0.211	-0.798	0.006	0.05
myci	occupancy	cov_pine	-0.176	0.17	-0.494	0.162	0.3
myci	occupancy	dist	-0.093	0.159	-0.385	0.253	0.559
myci	occupancy	forestenf	-0.72	0.244	-1.178	-0.203	0.003
myci	occupancy	forestplas	-1.445	0.309	-1.985	-0.823	0
myci	occupancy	forestsnf	-1.044	0.341	-1.632	-0.296	0.002
myci	detection	(Intercept)	-1.218	0.142	-1.476	-0.925	0
myci	detection	jday	0.405	0.162	0.089	0.697	0.012
myci	detection	length	0.224	0.166	-0.095	0.548	0.177
myci	detection	cc	-0.011	0.128	-0.274	0.218	0.933
myev	occupancy	ba_live	0.645	0.221	0.212	1.092	0.004
myev	occupancy	ba_snag	0.401	0.206	0.009	0.794	0.051
myev	occupancy	cov_pine	-0.203	0.182	-0.506	0.187	0.264
myev	occupancy	solrad	-0.059	0.195	-0.431	0.311	0.762
myev	occupancy	forestenf	1.263	0.271	0.754	1.851	0
myev	occupancy	forestplas	2.494	0.455	1.584	3.353	0
myev	occupancy	forestsnf	0.352	0.282	-0.149	0.911	0.212
myev	detection	(Intercept)	-0.185	0.055	-0.287	-0.082	0.001
myev	detection	jday	0.194	0.06	0.079	0.301	0.001
myev	detection	length	0.041	0.057	-0.078	0.133	0.472
myev	detection	cc	0.009	0.053	-0.095	0.1	0.861
mylu	occupancy	ba_snag	0.235	0.177	-0.149	0.562	0.183
mylu	occupancy	dist	0.086	0.151	-0.205	0.359	0.569
mylu	occupancy	solrad	0.257	0.165	-0.056	0.567	0.121
mylu	occupancy	forestenf	-0.359	0.224	-0.8	0.079	0.11
mylu	occupancy	forestplas	2.691	0.537	1.65	3.699	0

mylu	occupancy	forestsnf	-0.726	0.278	-1.282	-0.198	0.009
mylu	detection	(Intercept)	-0.207	0.069	-0.339	-0.072	0.003
mylu	detection	jday	0.021	0.073	-0.126	0.148	0.775
mylu	detection	length	-0.162	0.075	-0.306	-0.014	0.03
mylu	detection	cc	-0.165	0.087	-0.326	0.03	0.059
myth	occupancy	cov_fir	-0.413	0.142	-0.713	-0.15	0.004
myth	occupancy	dist	-0.193	0.148	-0.475	0.1	0.191
myth	occupancy	solrad	0.302	0.152	0.007	0.576	0.047
myth	occupancy	forestenf	0.688	0.227	0.255	1.131	0.002
myth	occupancy	forestplas	-0.76	0.236	-1.229	-0.286	0.001
myth	occupancy	forestsnf	0.5	0.297	-0.119	1.017	0.092
myth	detection	(Intercept)	-0.566	0.073	-0.703	-0.425	0
myth	detection	jday	-0.018	0.072	-0.15	0.126	0.806
myth	detection	length	0.213	0.083	0.054	0.35	0.01
myth	detection	cc	-0.06	0.079	-0.21	0.105	0.448
myyu	occupancy	cov_pine	-0.289	0.168	-0.626	0.025	0.086
myyu	occupancy	shrub_cov	-0.397	0.158	-0.708	-0.083	0.012
myyu	occupancy	tmx	0.256	0.169	-0.092	0.594	0.13
myyu	occupancy	forestenf	-0.005	0.259	-0.522	0.448	0.986
myyu	occupancy	forestplas	-0.248	0.286	-0.762	0.323	0.386
myyu	occupancy	forestsnf	-0.109	0.331	-0.722	0.525	0.742
myyu	detection	(Intercept)	-1.277	0.104	-1.482	-1.074	0
myyu	detection	jday	-0.004	0.104	-0.201	0.218	0.969
myyu	detection	length	0.152	0.103	-0.05	0.364	0.137
myyu	detection	cc	-0.107	0.104	-0.312	0.099	0.304
pahe	occupancy	cov_fir	-0.263	0.168	-0.582	0.065	0.117
pahe	occupancy	forestenf	0.489	0.264	0.017	1.032	0.065
pahe	occupancy	forestplas	-1.995	0.351	-2.673	-1.332	0
pahe	occupancy	forestsnf	0.137	0.31	-0.435	0.782	0.658
pahe	detection	(Intercept)	-1.213	0.114	-1.42	-0.98	0
pahe	detection	jday	0.198	0.119	-0.075	0.41	0.096
pahe	detection	length	0.21	0.117	-0.024	0.433	0.072
pahe	detection	cc	-0.201	0.117	-0.438	0.019	0.085