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Black-backed Woodpecker MIS Surveys on Sierra Nevada National Forests: 2012 Annual Report

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Black-backed Woodpecker.
Original artwork by Lynn Schofield.

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Summary

The Black-backed Woodpecker (*Picoides arcticus*) was selected by the Pacific Southwest Region of the USDA Forest Service as a Management Indicator Species (MIS) for snags in burned forests across the ten Sierra Nevada national forest units in the Pacific Southwest Region: Eldorado, Inyo, Lassen, Modoc, Plumas, Sequoia, Sierra, Stanislaus, Tahoe, and the Lake Tahoe Basin Management Unit. In 2008 The Institute for Bird Populations collaborated with Region 5 personnel to develop and field-tested survey procedures and collected preliminary information on Black-backed Woodpecker distribution across Sierra Nevada national forests. We used the findings from our 2008 pilot study to design a long-term MIS monitoring program for Black-backed Woodpecker across ten national forest units of the Sierra Nevada, which we have now implemented annually since 2009. The primary goal of the program is to monitor trends in the amount of recently burned forest on the study area's ten national forests that is occupied by Black-backed Woodpeckers, so that Forest Service personnel can evaluate the likely effects of forest plan implementation on Black-backed Woodpecker populations. Additional goals are to better understand Black-backed Woodpecker abundance, distribution, and habitat associations across the Sierra Nevada, to develop information that can inform effective conservation of Black-backed Woodpecker in the Sierra Nevada, and to collect and interpret information on other bird species utilizing burned forests.

During the 2012 field season, we used passive and broadcast surveys to assess Black-backed Woodpecker occupancy at 953 survey points arrayed across 52 recent fire areas (1-10 years post-fire) throughout our study area. Combined with data collected during 2009, 2010, and 2011, we now have broadcast surveys and habitat assessment data at 1599 unique survey points within 87 fire areas. We also collected on-the-ground habitat data at each survey point, and collated additional habitat data from remote-sensed GIS sources. In addition, we conducted passive point counts for other bird species at approximately half of the Black-backed Woodpecker survey points.

In 2012 we detected Black-backed Woodpeckers at 207 survey points distributed across 39 of the 52 fire areas we surveyed, including fire areas on all ten national forest units in our study area.

We detected Black-backed Woodpeckers on both the west and east sides of the Sierra Nevada crest, and across nearly the full latitudinal range of our study area.

Results were produced by three separate analyses, beginning with an exploration of annual changes in Black-backed Woodpecker occurrence within our sampling frame. To assess these changes, we used a hierarchical modeling approach that incorporated separate but linked models for the observation (detection) and state (occupancy) processes. Additionally, the state process was split into two hierarchical levels, to separately model whether a fire (or at least the portion of it we sampled) was occupied (fire-level occupancy) and whether survey points within a fire were occupied (point-level occupancy). For each occupancy probability model, we defined a logit-linear model that included covariates that we deemed important based on previous years' analyses. Fire age was the only fire-level covariate, while point-level covariates included latitude, snag density, burn severity, pre-fire canopy cover, and elevation. Detectability was modeled as a function of survey interval duration (2- vs. 3-minute), count type (passive vs. broadcast survey), and seasonality (day of year). Each survey year was modeled separately, providing independent but comparable models of true occurrence within each year's sampling frame.

Mean occupancy probability for points surveyed in 2012 was 0.24 (95% credible interval: 0.23 – 0.26), which overlaps with estimates for 2009 (mean: 0.25) but is higher than estimates for 2010 (mean: 0.19) and 2011 (mean: 0.21). These results suggest that occupancy was lower in 2010 and 2011 but fully rebounded in 2012. Assuming that our sample was representative of habitat yielded by all fires in the study area that burned in the 10 years prior, we estimate that approximately 58,443 ha of the 233,774 ha of burned forest on the ten national forest units within our sampling frame was occupied by Black-backed Woodpeckers in 2009 (95% CI: 51,430 – 72,470 ha), 41,024 ha of the 215,915 ha of burned forest was occupied in 2010 (95% CI: 36,707 – 45,342 ha), 37,183 ha of the 181,381 ha of burned forest was occupied in 2011 (95% CI: 32,649 – 45,531), and 67,208 ha of the 280,035 ha of burned forest was occupied in 2012 (95% CI: 64,408 – 72,809 ha).

Our second analysis used data from all four survey years (2009-2012) to explore occurrence dynamics over time, specifically the probabilities of colonization and extinction of Black-backed Woodpeckers at survey points and fires. Our top models of point-level colonization and extinction, as compared using the Akaike Information Criterion (AIC), strongly indicated that different parameters governed colonization dynamics versus extinction dynamics. The average probability of colonization by Black-backed Woodpeckers at a previously unoccupied point in any given year was modeled to be 7.8%, while the average probability that an occupied site would go extinct in any given year was 67%. The probability of extinction had no clear covariate relationships, with moderate support for negative relationships with increased burn severity and pre-fire canopy cover – extinction occurred less frequently at survey points with greater pre-fire canopy cover and greater burn severity. Colonization, however, had very strong relationships to two covariates. Colonization was more likely at early post-fire points and at points with higher densities of snags. At the youngest sites (1 year post-fire) with the greatest density of snags (~200 snags per hectare), the probability that an unoccupied point would become occupied the next year was just under 50%.

Our second analysis also modeled the probability of colonization and extinction at the scale of individual fires, exploring the effect of fire age, fire area, and survey year. Similar to the point-level analysis, colonization was strongly associated with fire age, while extinction was strongly associated with survey year (indicating year-specific or stochastic changes in extinction probability). The strong support for fire age as a covariate of colonization but not extinction in both point-level and fire-level analyses implies a fundamentally different dynamic governing Black-backed Woodpecker occupancy than previously considered: Black-backed Woodpeckers do not necessarily abandon sites because they are too old, but that old sites are less likely to be colonized by constantly moving woodpeckers.

Our third analysis focused on other bird species occupying recently burned forests. In addition to Black-backed Woodpeckers, our passive point counts combined across four years yielded detections of 149 other bird species within the fire areas. We used these data, combined at the scale of individual fires, to explore how bird communities change over time using ordination and indicator species analysis. Bird community ordination found that bird communities sorted significantly according to many factors, including mean live tree density, mean snag density, mean burn severity, heterogeneity in burn severity, mean pre-fire canopy cover, and fire age. We extended the analysis by further exploring the effect of fire age on structuring communities. In particular, we found that communities linearly differentiated themselves in the first 5 years post-fire, but there was no linear differentiation in years 6-10, indicating that bird communities do not change as rapidly over time during that period. This finding was confirmed via indicator species analysis, which found significant indicators for post-fire years 2, 4, 5, and 10. These years, consequently, can be seen as nodes, during which bird communities show temporally unique traits. Black-backed Woodpeckers were identified as a significant indicator for forests 4-years post-fire and showed low indicator values greater than 6 years post-fire. These trends, as well as species-specific analyses of environmental covariate relationships, confirm that post-fire bird species response is both individualistic and, in aggregate, generalizable by a number of environmental factors.

Introduction

The Black-backed Woodpecker (*Picoides arcticus*) is designated by the Pacific Southwest Region of the USDA Forest Service as a Management Indicator Species (MIS) for snags in burned forests across the ten Sierra Nevada national forest units in the Pacific Southwest Region: Eldorado, Inyo, Lassen, Modoc, Plumas, Sequoia, Sierra, Stanislaus, Tahoe, and the Lake Tahoe Basin Management Unit (USDA Forest Service 2007a, 2007b). The MIS approach identifies species whose population changes are believed to indicate the effects of management activities (USDA Forest Service 2007a). The habitat needs of MIS are to be considered in the establishment of forest plan objectives for important wildlife and fish habitat, and as forest plans are implemented through individual projects, Forest Service managers are to assess their effects on MIS habitat (USDA Forest Service 2007a). Additionally, MIS population monitoring is used to assess the outcomes of forest plan implementation, since it is impossible to monitor the status or population trend of all species (USDA Forest Service 2007a). Population monitoring is thus an integral component of the MIS approach.

Black-backed Woodpeckers are most abundant in stands of recently fire-killed snags (Hutto 1995, Kotliar et al. 2002, Smucker et al. 2005), although the species can be found in unburned forest stands throughout its range. Black-backed Woodpeckers foraging in burned forests feed primarily on wood-boring beetle larvae (Villard and Beninger 1993, Murphy and Lehnhausen 1998, Powell 2000), although some studies have also reported or inferred foraging on bark beetle larvae (Lester 1980, Goggans et al. 1988). Bark beetles and wood-boring beetles share important life-history characteristics (both spend a prolonged portion of their life-cycle as larvae inside dead or dying trees) but also exhibit differences that may be important in their ecological interactions with Black-backed Woodpeckers. Bark beetles are small (generally <6 mm in length), numerous, often able to attack live trees, and generally remain as larvae in bark less than a year before emerging as adults (Powell 2000). In contrast, wood-boring beetles have much larger larvae (up to 50 mm long), are less numerous, and can remain as larvae in dead wood for up to three years (Powell 2000). Additionally, most wood-boring beetles are unable to attack living trees, and concentrate heavily in fire-killed wood, which some genera have been shown to find by sensing smoke or heat (reviewed in Powell 2000). Black-backed Woodpecker preference for wood-boring beetles could thus either drive or result from the species' proclivity to forage and nest in or near forest stands that have recently burned.

Although Black-backed Woodpecker shows a strong association with burned stands of conifer forest, the species is not closely tied to any particular tree species or forest type. Studies from different parts of its range report preferential foraging on Lodgepole Pine (*Pinus contorta*; Bull et al. 1986, Goggans et al. 1989), spruce (*Picea* sp.; Villard 1994, Murphy and Lehnhausen 1998), White Pine (*Pinus strobus*; Villard and Beninger 1993), and in California, Red Fir (*Abies magnifica*; Raphael and White 1984).

In 2008 The Institute for Bird Populations collaborated with Region 5 personnel to develop and field-test survey procedures and collected preliminary information on Black-backed Woodpecker distribution across Sierra Nevada national forests (Siegel et al. 2008). We used the findings from the 2008 pilot study to design a long-term MIS monitoring program for Black-backed Woodpecker across ten national forest units of the Sierra Nevada. The primary goal of the program is to monitor trends in the amount of recently burned forest on the study area's ten national forests that is occupied by Black-backed Woodpecker, so that Forest Service personnel can evaluate the likely effects of forest plan implementation on Black-backed Woodpecker populations. Additional goals are to better understand Black-backed Woodpecker abundance, distribution, and habitat associations across the Sierra Nevada, to develop information that can inform effective conservation of Black-backed Woodpecker in the Sierra Nevada, and to collect information on other bird species utilizing burned forests. The Institute for Bird Populations collaborated with the Forest Service to initiate an annual Black-backed Woodpecker MIS monitoring program beginning in 2009 (Siegel et al. 2010, 2011, and 2012; Saracco et al. 2011), based on findings and recommendations in Siegel et al. (2008).

In 2012 we continued Sierra-wide MIS monitoring for Black-backed Woodpeckers. Here we detail the results of this fourth year of MIS monitoring in recently burned forest stands.

Methods

Sample Design

We used the GIS data layer VegBurnSeverity11_1.mdb (available from http://www.fs.usda.gov/detail/r5/landmanagement/gis/?cid=STELPRDB5327833), which indicates fire boundaries and fire severity of fires throughout California, to extract data for all fires that occurred between 2002 and 2011 and that included at least 50 ha of conifer forest that burned at mid-severity and/or high-severity on one or more of the ten national forest units in our study area.

We assigned fire areas that met our selection criteria, including fires that were sampled in previous years and fires that were new to the survey, to a random priority order. Our intention was to survey the first 50 fire areas on the list in 2012, but if that proved impossible, we would discard fire areas according the priority order, to avoid biasing the sample.

Data Collection

All data collection procedures remained consistent with protocol utilized during the 2011 field season, unless noted otherwise.

Establishing survey points. The fire areas we selected varied greatly in size, from 124 ha (2002 Showers Fire on Tahoe NF) to 61,261 ha (2002 McNally Fire on Sequoia NF). At the smaller fire areas, a 2-person team could easily saturate the fire area with survey effort in a single morning; however saturating the larger fire areas with survey effort could require weeks of work. We limited survey effort to what could be achieved by a 2-person team in one day, generally surveys at about 20 survey points.

For fires that we had not previously surveyed, we determined where within the fire area to place our survey points by using GIS to randomly select a ‘survey target point’ somewhere within the perimeter of each fire area, and indicating that point on field maps given to field crews. Crews were instructed to establish their survey points as close to the survey target point as possible, using the following rules:

1 – If trails or roads passed through the fire area, survey points were placed along them, such that the point along the road and trail network that was closest to the survey target point AND lay within low- mid- or high-severity burned conifer forest was included within a contiguous array of survey points, spaced 250 m apart. Survey points that were placed along a road were offset 50 m from the actual road in a randomly selected direction, unless only one side of the road was accessible (due to cliffs, for example) or only one side of a road was burned.

2 – If no trails or roads bisected the fire area, crews established an array of evenly spaced (250 m between points) off-trail survey points, as close to the target survey point as reasonably possible, without compromising safety or requiring additional days of hiking to access.

At the larger fire areas we thus sampled only a fraction of the total land area, but that fraction was randomly selected, within reasonable accommodations for accessibility and safety.

For fire areas that had been surveyed previously, we simply used the same survey points that were established previously by our field crews, using the placement rules described above. On rare occasions where survey points established previously were inaccessible due to changes in the landscape, later-lingering snowpack, etc., substitute points were established as close as possible to the previous points following the previously described rules.

Broadcast surveys. At each survey point we conducted a 6-min broadcast survey to elicit responses from Black-backed Woodpeckers. We used FoxPro ZR2 digital game callers to broadcast electronic recordings of Black-backed Woodpecker vocalizations and drumming. The electronic recording we broadcast was obtained from The Macaulay Library of Natural Sounds, Cornell Laboratory of Ornithology (G.A. Keller, recordist), and included the *scream-rattle-snarl* vocalization, *pik* calls, and territorial drumming.

We began the 6-min broadcast survey (Fig. 1) at each survey point by broadcasting the recording of Black-backed Woodpecker vocalizations and drumming for approximately 30 seconds at a standardized volume, and then quietly listening and watching for Black-backed Woodpeckers until two minutes had elapsed (including the 30-second broadcast period). At two minutes into the survey we again broadcasted the 30-second recording, and then quietly listened and watched until a total of four minutes had elapsed since the beginning of the survey, at which point we repeated the sequence of broadcasting and listening one more time, yielding three 2-min survey intervals. When Black-backed Woodpeckers were detected, we recorded their initial distance and bearing from the observer, whether species identification was confirmed visually, age (adult or juvenile) and sex (male, female, or unknown) of each bird, and whether the individual performed territorial drumming or vocalized. Black-backed Woodpecker surveys generally began within 10 min of official local sunrise, and were always completed by 3.5 h after sunrise.

Passive surveys and multi-species point counts. At 459 of the survey points (generally every second point along each transect), we *preceded* the broadcast survey with a 7-min passive point count to count all birds of any species (including Black-backed Woodpecker). The 7-min point count consisted of a 3-min interval immediately followed by two 2-min intervals (Fig. 1). Division of the count into discrete detection intervals yields information for assessing detection probability of Black-backed Woodpeckers. Observers estimated the horizontal distance, to the nearest meter, to each bird detected. Estimating distance to each bird provides additional information for estimating detection probability in a distance sampling framework (Buckland et al. 2001). The observers also recorded whether each bird ever produced its territorial song during the point count. Additional details of the point count methods are provided in Siegel et al. (2010).

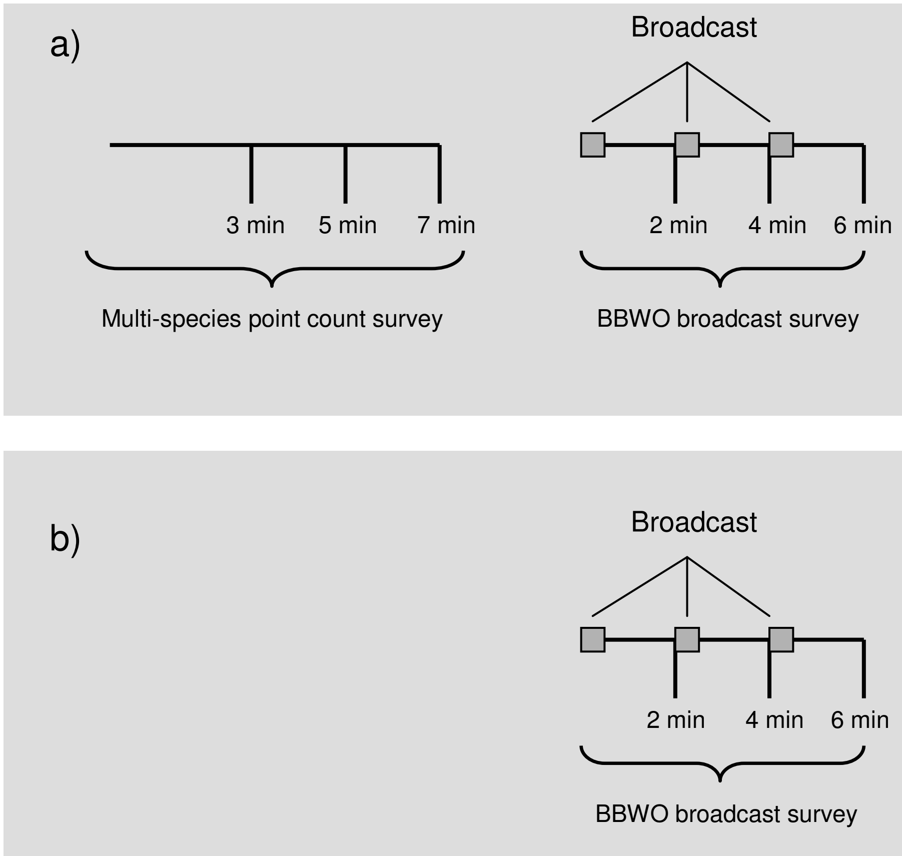

Figure 1. Schematic diagram of our survey methodology for detecting Black-backed Woodpeckers. Dark gray squares indicate period of actively broadcasting Black-backed Woodpecker drumming and vocalizations; black line segments indicate periods of passive observation. Observers alternated between both passive and broadcast (a) and broadcast-only (b) methods at successive survey points.

Habitat and other ancillary data. After completing point counts and broadcast surveys each day, observers returned to the survey points to collected cursory habitat data. In addition to recording UTM coordinates, they classified the habitat within a 50-m radius plot centered on the survey point, according to the California Wildlife Habitat Relationships (CWHR) habitat classification system (California Department of Fish and Game 2005). They also characterized the abundance and size of snags within the plot, estimated basal area of snags and live trees using a 10 BAF timber-cruising crutch, recorded the dominant pre-fire habitat type, and used CWHR-defined categories to classify the dominant tree size (including snags) and amount of remaining live canopy cover. Additional details of the methods for collecting habitat data are provided in Siegel et al. (2010).

Data Analysis

Goals and analysis structure. Based on previous analyses of the MIS data (Siegel et al. 2012), our analytical goals for the 2012 data centered on formalizing analyses begun in 2011 to capitalize on the extended time-series of monitoring data. Specifically, our analysis focuses on answering three questions:

(1) What is the overall proportion of fires and points in the sampling frame occupied in 2012 and how does this compare to previous years?

(2) What are the probabilities of colonization and extinction at sites, and how have they changed over time and with site-specific environmental factors?

(3) What can we learn about overall bird community composition and structure at recently burned sites?

Question 1 builds extensively on previous work, provides a model for future annual assessments, and is the central question that this monitoring program was implemented to answer. Question 2 allows a greater understanding of the dynamics underlying changes in Black-backed Woodpecker occurrence. Goal 3 builds upon previous analyses (Siegel et al. 2011, 2012) to further explore post-fire bird communities and how community structure relates to Black-backed Woodpecker occurrence. Descriptions of the methods used in addressing each of these questions follow this section.

Based on previous modeling work with the 2009-2011 MIS monitoring data, we examined the relationship between occupancy and occupancy dynamics with the following environmental and site characteristics:

- Latitude (in decimal degrees) recorded from USGS topographic maps.
- Elevation, collected in the field from GPS and USGS topographic maps but formalized from intersecting GPS points with a 30-m resolution California DEM (Gesch 2007, Gesch et al. 2002). In models we used the residuals of a regression of elevation on latitude, thereby

controlling for the downslope bias in elevational ranges as latitude increases (Saracco et al. 2011, Siegel et al. 2011).

- Density of snags (standing dead trees) recorded at the survey point. Snag counts were conducted immediately after completing woodpecker surveys at burned sites and consisted of counting all snags of different size classes (10-30, 30-60, and >60 cm dbh) within 50 m of each survey point. Size-specific snag counts were aggregated in the field into different categories (≤5, 6-15, 16-30, 31-50, 51-100, >100 stems per plot), which were converted to numerical quantities (1, 6, 16, 31, 51, 101, respectively) for analysis. Counts across all three size classes were summed and snag density (snags/ha) was calculated.
- Density of live trees recorded at the survey point. Live tree density was calculated from vegetation survey data using the same methods as snag density.
- Pre-fire % tree cover calculated from 100-m resolution California Multi-source Land Cover Data (http://frap.cdf.ca.gov/data/frapgisdata/download.asp?spatialdist=1&rec=fveg02_2). We calculated this variable by averaging midpoints of the % tree cover variable (WHRDENSITY) at 100 m buffers around survey points.
- Number of years since fire (range = 1 to 10 years).
- Change in percent canopy cover (a measure of burn severity) based on satellite derived relativized difference normalized burn ratio score RdNBR (Miller et al. 2009). Values of *cc* were summarized at 90-m^2 resolution by averaging 30-m^2 values from GIS layers provided by the US Forest Service (J. D. Miller) using the 'raster' package in R (Hijmans and Etten 2012).

Modeling annual occupancy. Occupancy models allow the estimation of the true presence (or occupancy) of a species at a location, unbiased by false absences. As survey data inherently contain an unknown quantity of false absences (i.e., non-detections when the species was truly present), it is critical that survey data be interpreted only after accounting for false absences. The framework presented here builds on the framework developed in the 2011 MIS report (Siegel et al. 2012) and published by Saracco et al. (2011). As presented in the 2011 MIS report (Siegel et al. 2012), given 3 (or more) years of sampling, combining all data into one model is not advantageous due to pseudoreplication of treating yearly surveys at the same sites as independent occurrence samples. A dynamic occupancy modeling framework (MacKenzie et al. 2003) allows the annual modeling of occupancy within one model, and avoids pseudoreplication, but that framework prioritizes the modeling of colonization and extinction probabilities, leaving annual occupancy solely as a derived parameter. When occupancy is a derived parameter, one cannot explicitly model relationships between it and other factors, such as environmental covariates. Thus, we prefer not to use dynamic occupancy models for direct inference on annual changes in occupancy. While we present a dynamic occupancy analysis here (see *Modeling dynamic occupancy*), for consistency in occurrence estimates across yearly reports, we also present results of single-year occupancy models for each of the four years of monitoring that have now been completed. The drawback of using multiple single-year occupancy models is that covariate relationships will be modeled independently for each year, yielding different occupancy estimates than if all years were pooled into a single model. However, combined with modeling of occupancy dynamics, we believe this to be a strong framework for the analysis of trends over time.

Our annual model of occupancy was based from data on $i = 1,\ldots,N$ survey points, $j = 1,\ldots,M$ fire areas, and $k = 1,\ldots,K$ survey intervals, with values for N, M, and K, unique to survey year. For the four years of monitoring, these values were: 899, 860, 895, and 953 for N points in 2009, 2010, 2011, and 2012, respectively; 51, 49, 50, and 52 for M fire areas; and 5, 9, 6, and 6 for K survey intervals (combined passive surveys with 3 broadcast surveys).

The observational data for our model consisted of encounter histories for each survey point. In 2009, our field protocol consisted of what might be called a 'double' removal design (Farnsworth et al. 2002), such that only the first interval of encounter was recorded for the passive count intervals, and the count was discontinued following a detection on the broadcast count intervals. In 2010 - 2012, a full detection history recording all detections or non-detections was recorded for all passive survey intervals, while the removal design (i.e., discontinuing counts following the initial broadcast-based detection) was used for broadcast intervals. This sampling framework resulted in 32 possible detection histories for 2012, the results of which are summarized in Table 1. Tables of encounter histories for previous years can be found in previous annual reports (Siegel et al. 2010, 2011, 2012).

Table 1. Encounter history frequencies (numbers of survey points) in the 2012 Black-backed Woodpecker survey data. For passive surveys, the total number of survey intervals that one or more Black-backed Woodpeckers were detected in is listed (passive surveys were only conducted at approximately half of points). For broadcast survey capture histories, ones indicate detections, zeros indicate non-detections, and NAs indicate missing data (by design, see text for detail). Overall, Black-backed Woodpeckers were detected at 207 of the 953 points that we surveyed in 2012.

Number of passive detections	Broadcast History			Frequency
	Interval 1	*Interval 2*	*Interval 3*	
-	0	0	0	389
-	0	0	1	14
-	0	1	NA	22
-	1	NA	NA	69
0	0	0	0	357
0	0	0	1	9
0	0	1	NA	12
0	1	NA	NA	32
1	0	0	0	8
1	0	0	1	2
1	0	1	NA	3
1	1	NA	NA	7
2	0	0	0	3
2	0	0	1	2
2	0	1	NA	1
2	1	NA	NA	5
3	0	0	0	3
3	0	0	1	1
3	0	1	NA	3
3	1	NA	NA	11

To model annual occupancy, we used a hierarchical modeling framework (Royle and Dorazio 2008) to build separate but linked models for the observation (detection) and state (occupancy) processes. Our occupancy model structure identically followed that described in the 2011 analysis (Siegel et al. 2012). This structure subdivides the state (i.e., true occurrence) observation into two hierarchical levels separating the processes that determine whether a fire is occupied (more accurately, the portion of a fire surveyed by all points), and the processes that determine whether a point is occupied. This separation of fire-level and point-level occupancy processes better describe the heterogeneity of the system and the observed dynamics of woodpecker occupancy.

For each year of data, the same set of covariates was used for the modeling of occupancy (both fire-level and point-level) and detectability. Detectability was modeled as a function of survey interval duration (3-minute or 2-minute), survey type (passive or broadcast), and day of year. Fire-level occupancy was modeled as a function of fire age but was also allowed a random fire-level effect (Saracco et al., 2011). Point-level occupancy was modeled as a function of latitude, elevation, snag density, pre-fire canopy cover, and burn severity (see *Goals and analysis structure*, above).

We implemented a Bayesian analysis of the model using Markov chain Monte Carlo (MCMC) methods (Gilks et al. 1996) in the software package WinBUGS (Spiegelhalter et al. 2003). We used vague prior distributions for all model parameters. For all covariate effects in the model we used Norm(0, 0.001) priors. We assigned a prior of Norm(0, $1/\sigma_f^2$) for the random point effect (fire$_j$) in the model for ω_j, and a prior of Unif(0,10) for the variance parameter σ_f. For the intercepts of the p and ψ models, we defined priors for inverse-logit transformed parameters using Unif(0, 1). We conducted the WinBUGS analysis from R (R Development Core Team 2012) using the R2WinBUGS package (Sturtz et al. 2005). Further details of model structure and parameterization, are provided in our 2010 and 2011 analyses (Siegel et al. 2011, 2012).

Modeling point-level dynamic occupancy. Detectability, initial occupancy, colonization and extinction of Black-backed Woodpeckers at survey points over time were modeled using a dynamic occupancy framework (MacKenzie et al. 2003). In this framework, initial occupancy (ψ_0) is modeled for all survey points in the first year of sampling (here, 2009), and then the occurrence status is allowed to change among years according to an estimated probability of colonization (γ) or extinction (ε). Thus, the probability of occupancy at time t is dependent on both the initial occupancy probability as well as the probability (combined γ and ε) that the point has transitioned states from time 0 to time t.

In this framework, ψ has a slightly different interpretation from the previous analysis (*Modeling annual occupancy*). First, as the focus was on colonization and extinction dynamics, occupancy was modeled only at the point level (i.e., no fire-level occupancy) and occurrence at neighboring points within the same fire were assumed to be independent (i.e., no random effect of fire). This assumption facilitates implementation, but we intend to add in the random effect of fire beginning with our 2013 analysis. Second, in a dynamic framework, average occupancy for year *t* is based upon the total number of points that are surveyed across all years, not the total number of points that were actually surveyed in year *t*. In other words, the dynamic framework estimates occupancy in any year across all 1599 survey points, not the ~850-950 that were actually visited in any given survey season. As occupancy estimates are always proportions, the occupancy estimates derived from the two analyses will always be different due to different denominators within the occupancy proportions. Thus, care needs be taken when comparing occupancy estimates derived from the two analyses.

Dynamic occupancy modeling was conducted in a likelihood-based framework, whereby different competing models were built and their relative strength was measured using the Akaike Information Criterion (AIC; Burnham and Anderson 2002). In this model selection framework, competing models are built using all possible combinations of *a priori* selected variables. Since four variables can be parameterized (p, ψ_0, γ, and ε), this can lead to an untenable number of competing models. Thus, we used a two-step process, through which the best parameterization for p and ψ_0 was determined by AIC, and then that single parameterization was used for all competing models of γ and ε. Similar to the previous analysis, for detectability we investigated the effect of interval duration, survey type and day of year. For initial occupancy, we only investigated the effect of elevation (including quadratic effects) and latitude. Combined, these factors resulted in 56 competing models which were combined with null (i.e., random) model parameterizations for colonization and extinction. All 56 models were run and the best supported model was selected as the one with the lowest AIC.

Following selection of the best supported parameterization for detectability and initial occupancy, this parameterization was used to compare differently parameterized models of colonization and extinction. We tested the effects of snag density, fire age, burn severity, and pre-fire canopy cover as potential covariates for both colonization and extinction. Including models with multiple covariates, this resulted in 256 uniquely parameterized competing models, each with the same initial occupancy and detectability covariates, but with different colonization and extinction covariates. Support within the data for each model was determined through comparisons of AIC.

All models were run in R version 2.15 (R Core Development Team 2011) using the package 'unmarked' (Fiske and Chandler 2011).

Modeling fire-level dynamic occupancy. Different factors may influence colonization and extinction dynamics at different spatial scales. To investigate this, dynamic occupancy models were also run at the scale of individual fires. In this case, all survey points within a fire were aggregated within survey interval units. Thus, if a Black-backed Woodpecker was recorded at any of the up to 20 survey points within the first 3-minute passive survey interval, then a 1 (presence) was denoted for that interval. Survey points were similarly aggregated for all other passive and broadcast survey intervals.

Similar to the previous analysis, detectability, initial occupancy, colonization and extinction of Black-backed Woodpeckers over time were modeled using a dynamic occupancy framework (MacKenzie et al. 2003). A two-step analysis was conducted, first comparing covariates of initial occupancy and detectability and subsequently comparing covariates of extinction and colonization. Detectability and occupancy covariates for the fire-level analysis were the same as those used in the point-level occupancy analysis. Elevation and latitude covariates were constructed for the fire-scale by averaging values across all survey points within each fire. Colonization and extinction models evaluated three covariates: fire area (total hectares burned, information from USDA Forest Service), survey year[1] (2009 vs 2010 vs 2011), and fire age. A full model set was constructed evaluating all combinations and additive effects with the exception that year and fire age were not tested within the same model parameter (i.e., colonization or extinction) due to circularity.

[1] Colonization and extinction require two years (a "before" and an "after") to be modeled. Thus, given 4 years of sampling, only 3 years of either colonization or extinction can be modeled. Thus, the covariate for survey year only considers 3 years.

Modeling community occupancy. Building on the analysis of multi-species point count data from past years (Siegel et al. 2012), we sought to further explore how burned forest communities change in the 10 years post-fire and what bird species are strongly associated with Black-backed Woodpeckers during this time. Rather than repeat the multi-species hierarchical occupancy model explored previously (Siegel et al. 2012), we employed traditional tools of community ecology – ordination and indicator species analysis – to elicit new insights from the data.

To explore how community similarity was structured in environmental space, we used Nonmetric Multidimensional Scaling (NMDS, Kruskal 1964). NMDS takes ranked distances between sample units and uses an iterative process to ordinate units in multidimensional space (McCune and Grace 2002). In this case, fires in each survey year were used as sample units. As multi-species point counts were conducted at points within a fire, occurrences of species at individual points were summed across all points within each fire to create a fire-specific index of abundance for all species. To partially control for detectability, only individuals detected within 100 m of each point count station were used in the analysis. This resulted in relative abundances for 126 species of birds recorded at 202 fire-year sample units. Community dissimilarity was measured using the Bray-Curtis distance (Bray and Curtis 1957). Following ordination, NMDS axes were regressed against six environmental variables calculated at the fire-year level: mean live tree density, mean snag density, mean pre-fire canopy cover, mean burn severity, heterogeneity (standard deviation) in burn severity, and fire age. Ordination analyses were conducted in R version 2.15 using the package 'vegan' (Oksanen et al. 2013) and 'MASS' (Venables and Ripley 2002).

Indicator species analysis (Dufrene and Legendre 1997) was used to further explore how bird communities changed with years-since-fire. In particular, we were interested in determining which species were most strongly associated with forests of different fire ages, and particularly, where Black-backed Woodpeckers fell along this spectrum. Indicator species analysis calculates a single index for each species within each treatment (here, each year, 1-10 years post-fire) that shows the strength of association for that species with each treatment. Indicator values are based on both abundance (the number of individuals in a treatment) and fidelity (how unique a species is to a specific treatment). In this case, we tested how strongly different species indicated for specific years post-fire. Values range from 0 to 100, with 0 being no association. Significance of indicator values was assessed using Monte Carlo simulations with 1000 iterations to assess the probability of obtaining as high an indicator value as observed at random over the specified number of iterations (Dufrene and Legendre 1997).

Results

Scope of Survey Work Completed

In 2012 we completed surveys fully to protocol at 52 fire areas (Table 2), including broadcast surveys and habitat assessments at 953 survey points and passive, multi-species point counts at 459 of those points. All surveys were conducted between 9 May and 1 July, 2012. Combined with data collected during 2009, 2010, and 2011, we now have broadcast surveys and habitat assessment data at 1599 unique survey points within 87 fire areas. We provide summary information about fire areas surveyed once or more between 2009 and 2012 in Table 2.

Black-backed Woodpecker Detections

In 2012 we detected Black-backed Woodpeckers at 207 survey points distributed across 39 of the 52 fire areas we surveyed (Figs. 2-4). We detected Black-backed Woodpeckers on all ten of the national forest units in our study area. As was the case in previous years, we detected Black-backed Woodpeckers on both the west and east sides of the Sierra crest, and across nearly the full latitudinal range of our study area, including the most northerly fire area we surveyed (the Fletcher fire area on the Modoc NF, which spans the California – Oregon border; Fig. 2), and the second most southerly fire area we surveyed (the Vista fire area on the Sequoia NF; Fig. 5). We provide UTM coordinates and survey history of all survey points on an interactive, online map at: http://www.birdpop.net/index.php/viewmaps?catid=2&id=10:bbwomap.

Table 2. Summary information for each fire area surveyed once or more during the 2009 – 2012 field seasons of Black-backed Woodpecker MIS monitoring on Sierra Nevada national forests.

Primary national forest	Fire name	Year of fire	Burned area (ha)[1]	Dominant pre-fire habitat[2]	No. points (2009)	No. points (2010)	No. points (2011)	No. points (2012)
Eldorado	Freds	2004	1814	Sierra Mixed Conifer	20	0	19	20
Eldorado	Plum	2002	417	Sierra Mixed Conifer	12	12	12	13
Eldorado	Power	2004	5538	Sierra Mixed Conifer	20	20	20	20
Eldorado	Star	2001	4979	Sierra Mixed Conifer	0	20	20	0
Inyo	Azusa	2000	164	Pinyon-Juniper	8	0	0	0
Inyo	Birch	2002	1117	Pinyon-Juniper	19	0	0	0
Inyo	Crater	2001	1118	Jeffrey Pine	20	20	20	0
Inyo	Dexter	2003	1022	Jeffrey Pine	16	16	0	16
Inyo	Inyo Complex	2007	7574	Ponderosa Pine	16	0	0	0
Inyo	McLaughlin	2001	939	Jeffrey Pine	0	13	13	0
Inyo	Sawmill 00	2000	144	Ponderosa Pine	5	0	0	0
Inyo	Sawmill 06	2006	2452	Pinyon-Juniper	0	0	19	0
Inyo	Summit	2003	2474	Jeffrey Pine	0	0	16	0
Lassen	Brown	2009	684	Sierra Mixed Conifer	0	20	20	20
Lassen	Cone	2002	703	Jeffrey Pine	21	0	21	0
Lassen	Corral	2008	1952	Eastside Pine	0	0	0	20
Lassen	Cub	2008	6093	Sierra Mixed Conifer	0	20	20	15
Lassen	Onion 2	2008	1067	Sierra Mixed Conifer	0	20	20	20
Lassen	Peterson Complex	2008	1161	Eastside Pine	20	20	20	20
Lassen	Straylor	2004	996	Eastside Pine	0	0	0	20
Lassen	Sugar Loaf	2009	3127	Sierra Mixed Conifer	0	21	21	21
Modoc	Bell	2001	1260	Juniper	20	20	20	0
Modoc	Bell West	1999	773	Eastside Pine	21	0	0	0
Modoc	Blue	2001	13329	Eastside Pine	20	20	20	0
Modoc	Cougar	2011	749	Ponderosa Pine	0	0	0	20
Modoc	Fletcher	2007	916	Eastside Pine	19	17	19	20

Primary national forest	Fire name	Year of fire	Burned area (ha)[1]	Dominant pre-fire habitat[2]	No. points (2009)	No. points (2010)	No. points (2011)	No. points (2012)
Modoc	High	2006	421	Eastside Pine	0	19	19	19
Plumas	Antelope Complex	2007	9297	Eastside Pine	21	21	21	21
Plumas	Belden	2008	224	Sierra Mixed Conifer	0	13	13	13
Plumas	Boulder Complex	2006	1475	Eastside Pine	20	20	0	0
Plumas	Bucks	1999	11325	Sierra Mixed Conifer	20	0	0	0
Plumas	Cold	2008	2327	Sierra Mixed Conifer	0	0	0	19
Plumas	Devils Gap	1999	612	Sierra Mixed Conifer	20	0	0	0
Plumas	Fox	2008	1007	Sierra Mixed Conifer	0	0	18	0
Plumas	Frey	2008	4406	Sierra Mixed Conifer	0	20	18	0
Plumas	Grease	2006	163	Eastside Pine	0	0	0	17
Plumas	Horton 2	1999	1637	Sierra Mixed Conifer	20	0	0	0
Plumas	Lookout	1999	1009	Sierra Mixed Conifer	21	0	0	0
Plumas	Moonlight	2007	18864	Eastside Pine	20	20	20	20
Plumas	Pidgen	1999	1859	Sierra Mixed Conifer	18	0	0	0
Plumas	Pit	2008	9142	Sierra Mixed Conifer	0	0	0	20
Plumas	Rich	2008	2360	Sierra Mixed Conifer	21	21	0	21
Plumas	Scotch	2008	5647	Sierra Mixed Conifer	21	21	0	21
Plumas	Silver	2009	140	Sierra Mixed Conifer	0	0	11	11
Plumas	Storrie	2000	21117	Red Fir	15	0	0	0
Plumas	Stream	2001	1507	Eastside Pine	20	20	15	0
Sequoia	Albanita	2003	958	Jeffrey Pine	21	21	21	21
Sequoia	Broder Beck	2006	1457	Jeffrey Pine	0	20	20	20
Sequoia	Clover	2008	6088	Jeffrey Pine	0	20	20	20
Sequoia	Comb	2005	480	Sierra Mixed Conifer	0	0	0	20
Sequoia	Cooney	2003	841	Sierra Mixed Conifer	0	0	0	20
Sequoia	Crag 04	2004	364	Jeffrey Pine	19	0	18	19
Sequoia	Crag 05	2005	611	Jeffrey Pine	21	20	21	21
Sequoia	Deep	2004	1305	Sierra Mixed Conifer	11	11	11	11

Primary national forest	Fire name	Year of fire	Burned area (ha)[1]	Dominant pre-fire habitat[2]	No. points (2009)	No. points (2010)	No. points (2011)	No. points (2012)
Sequoia	Granite	2009	607	Jeffrey Pine	0	20	20	0
Sequoia	Highway	2001	1384	Mixed Hardwood-Conifer	0	0	20	0
Sequoia	Hooker	2003	1004	Jeffrey Pine	20	16	20	20
Sequoia	Lion	2009	1075	Red Fir	0	20	20	20
Sequoia	Lion 11	2011	7993	Sierra Mixed Conifer	0	0	0	20
Sequoia	Manter	2000	22450	Pinyon-Juniper	21	20	0	0
Sequoia	McNally	2002	61261	Sierra Mixed Conifer	19	17	16	17
Sequoia	Piute 08	2008	13516	Jeffrey Pine	20	19	0	0
Sequoia	Sheep	2010	2428	Sierra Mixed Conifer	0	0	0	20
Sequoia	Shotgun	2009	403	Sierra Mixed Conifer	0	0	0	16
Sequoia	Tamarack	2006	1911	Sierra Mixed Conifer	0	0	0	20
Sequoia	Vista	2007	180	Red Fir	19	19	19	19
Sierra	Motor	2011	2038	Blue Oak - Foothill Pine	0	0	0	24
Sierra	North Fork	2001	1614	Sierra Mixed Conifer	20	13	8	0
Sierra	Oliver	2008	1099	Sierra Mixed Conifer	0	0	17	0
Sierra	Tehipite	2008	3112	Sierra Mixed Conifer	0	0	0	21
Stanislaus	Hiram	1999	1144	Jeffrey Pine	10	0	0	0
Stanislaus	Kibbie	2003	1501	Sierra Mixed Conifer	21	0	21	21
Stanislaus	Knight	2009	2140	Sierra Mixed Conifer	0	19	19	19
Stanislaus	Mountain	2003	1747	Red Fir	0	12	12	9
Stanislaus	Mud	2003	1803	Red Fir	21	20	21	21
Stanislaus	Whit	2003	438	Red Fir	20	0	20	19
Stanislaus	White	2001	107	Sierra Mixed Conifer	8	8	8	0
Tahoe	Bassetts	2006	1006	Sierra Mixed Conifer	18	18	0	19
Tahoe	Fall	2008	584	Sierra Mixed Conifer	10	10	10	10
Tahoe	Gap	2001	574	Sierra Mixed Conifer	0	20	19	0
Tahoe	Government	2008	7784	Sierra Mixed Conifer	19	19	19	0
Tahoe	Harding	2005	616	Eastside Pine	21	21	21	20

Primary national forest	Fire name	Year of fire	Burned area (ha)[1]	Dominant pre-fire habitat[2]	No. points (2009)	No. points (2010)	No. points (2011)	No. points (2012)
Tahoe	Peavine	2008	192	Sierra Mixed Conifer	16	0	0	0
Tahoe	Treasure	2001	143	Eastside Pine	10	10	0	0
Tahoe Basin	Angora	2007	1146	Sierra Mixed Conifer	19	12	19	19
Tahoe Basin	Gondola	2002	165	Red Fir	12	12	0	12
Tahoe Basin	Showers	2002	125	Sierra Mixed Conifer	9	9	0	8

[1]Burned area represents only the total area of the fire within National Forest boundaries.

[2]Habitat classifications follow California Habitat Relationships (CWHR; California Department of Fish and Game 2005), and indicate the primary pre-fire habitat at the greatest number of survey points in a particular fire area, based on our own on-the-ground assessments.

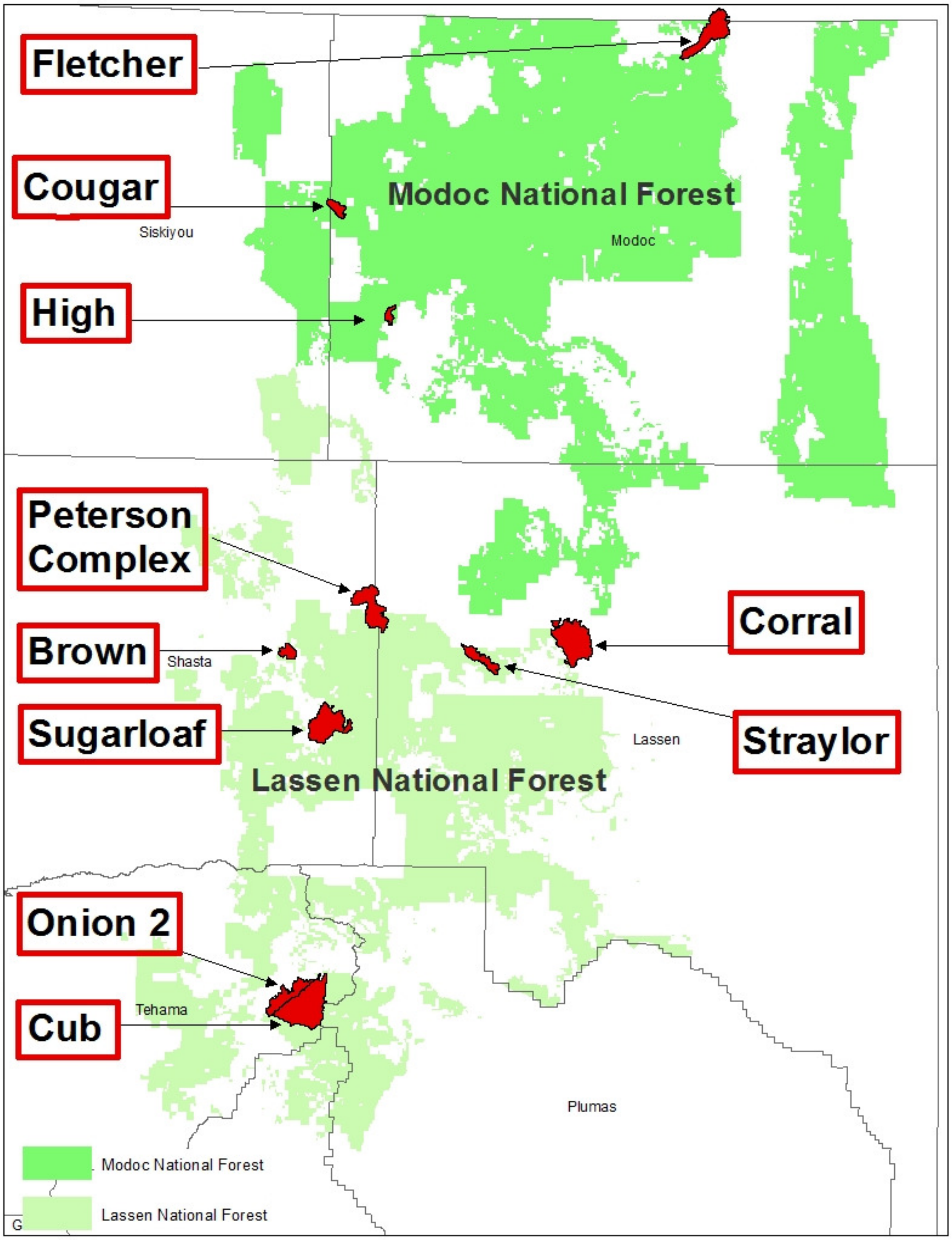

Figure 2. Fire areas (red shading) on the Modoc and Lassen National Forests that we surveyed for Black-backed Woodpeckers during the 2012 Black-backed Woodpecker MIS monitoring field season. Names of fire areas where Black-backed Woodpeckers were detected are enclosed in red boxes. Fire area names without red boxes indicate that no Black-backed Woodpeckers were detected; note that lack of detection does not necessarily mean Black-backed Woodpeckers were absent (see text for discussion of detection probability during this survey).

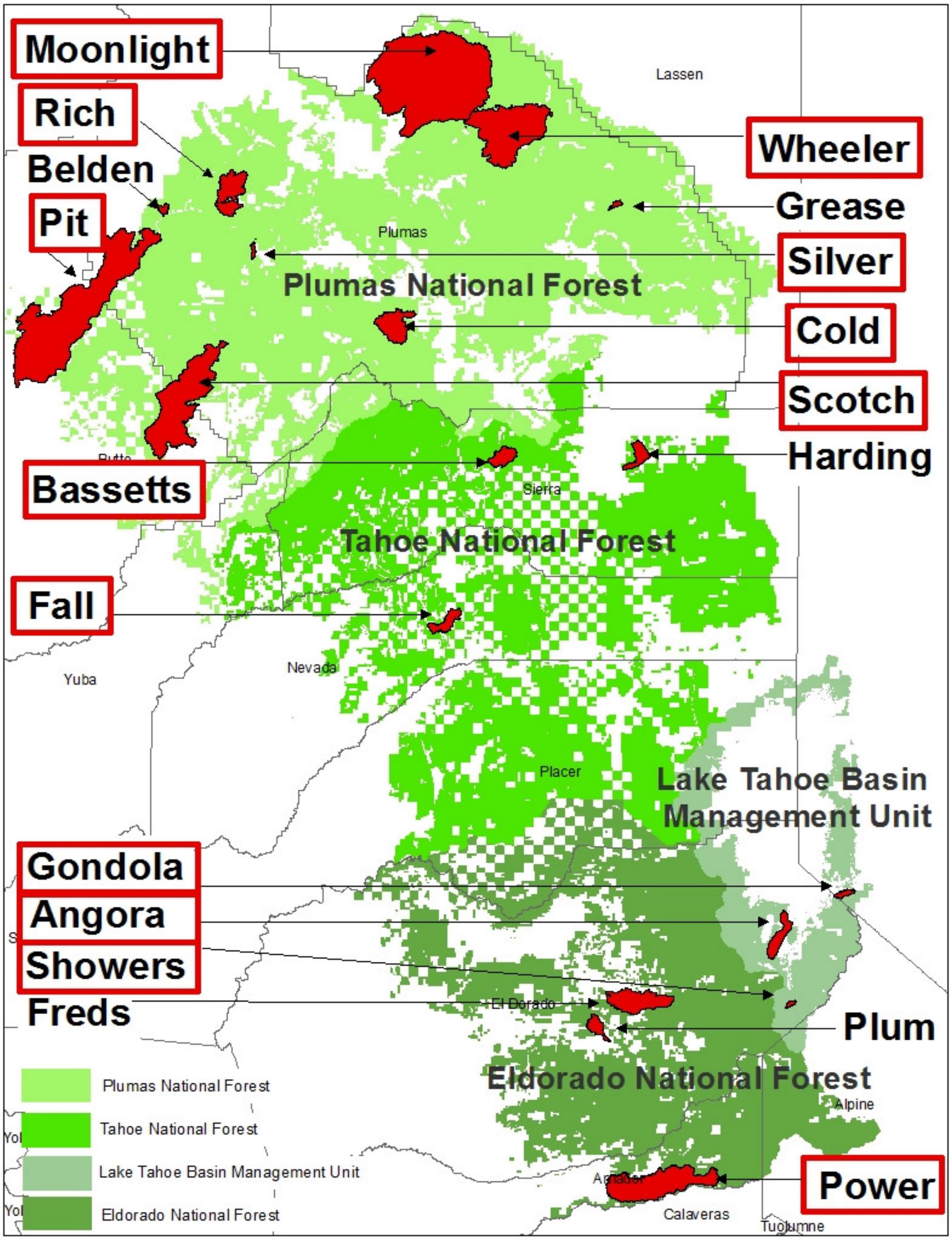

Figure 3. Fire areas (red shading) on the Plumas, Tahoe, and Eldorado National Forests and the Lake Tahoe Basin Management Unit that we surveyed for Black-backed Woodpeckers during the 2012 Black-backed Woodpecker MIS monitoring field season. Names of fire areas where Black-backed Woodpeckers were detected are enclosed in red boxes. Fire area names without red boxes indicate that no Black-backed Woodpeckers were detected; note that lack of detection does not necessarily mean Black-backed Woodpeckers were absent (see text for discussion of detection probability during this survey).

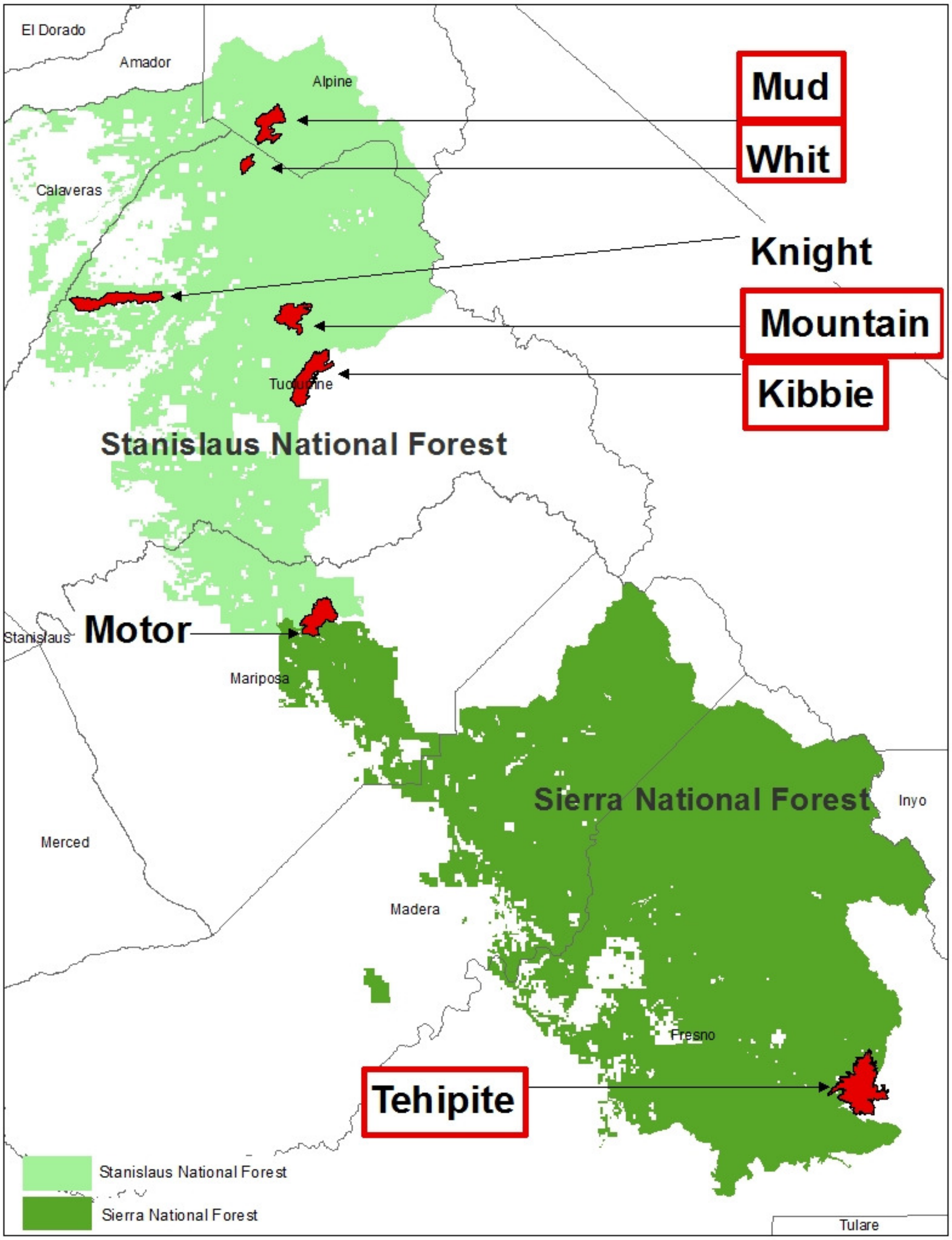

Figure 4. Fire areas (red shading) on the Stanislaus and Sierra National Forests that were surveyed for Black-backed Woodpeckers during the 2012 Black-backed Woodpecker MIS monitoring field season. Names of fire areas where Black-backed Woodpeckers were detected are enclosed in red boxes. Fire area names without red boxes indicate that no Black-backed Woodpeckers were detected; note that lack of detection does not necessarily mean Black-backed Woodpeckers were absent (see text discussion of detection probability during this survey).

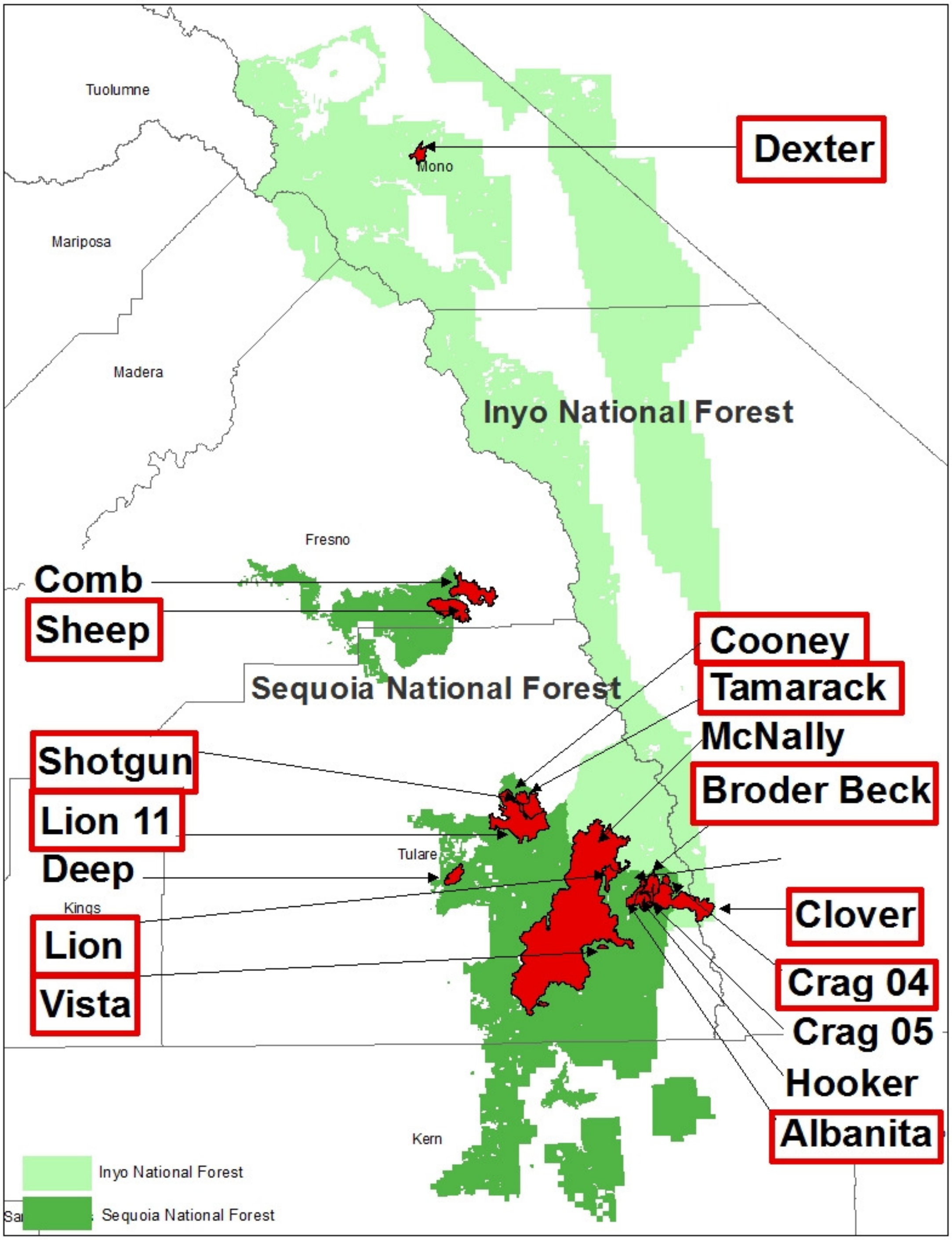

Figure 5. Fire areas (red shading) on the Inyo and Sequoia National Forests that were surveyed for Black-backed Woodpeckers during the 2012 Black-backed Woodpecker MIS monitoring field season. Names of fire areas where Black-backed Woodpeckers were detected are enclosed in red boxes. Fire area names without red boxes indicate that no Black-backed Woodpeckers were detected; note that lack of detection does not necessarily mean Black-backed Woodpeckers were absent (see text discussion of detection probability during this survey).

Analysis of Annual Occupancy

Mean occupancy probability for points surveyed during 2012 was 0.240 (95% credible interval: 0.23 – 0.26), which overlaps with our estimate for 2009 (95% CI: 0.22 – 0.31), but is significantly greater than estimates for 2010 (95% CI: 0.17 – 0.21) and 2011 (95% CI: 0.18 – 0.24) (Figure 6). Assuming that our sample was representative of woodpecker habitat yielded by fire areas that burned in the 10 years prior to each survey year, we estimate that approximately 67,208 ha (i.e., 24%) of the 280,035 ha of burned forest on the ten national forest units within our sampling frame were occupied by Black-backed Woodpeckers in 2012 (or a range based on the 95% credible interval of 64,408 – 72,809 ha) compared to an estimate of 58,443 ha of 233,774 ha occupied in 2009, 41,024 ha of 215,915 ha occupied in 2010, and 37.183 ha of 181,381 ha occupied in 2011. Table 3 summarizes detections and predicted occupancy probabilities for each fire area surveyed in 2009 through 2012.

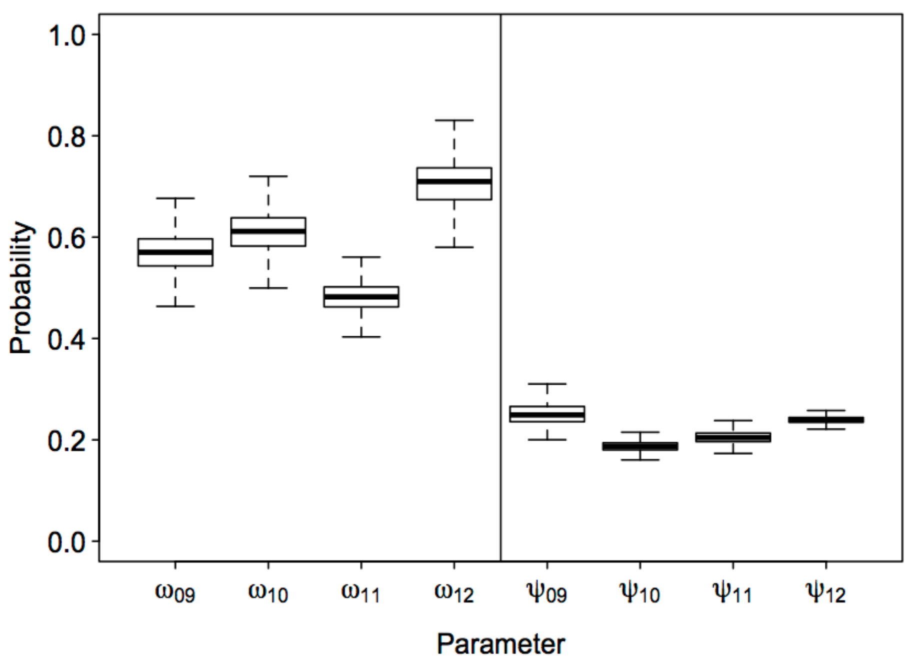

Figure 6. Mean probability of fire-level (ω) and point-level (ψ) occupancy for Black-backed Woodpeckers as modeled from individual year-based hierarchical models. Plots show median (bold line), 95% quantiles (box) and full range (whiskers) of posterior distribution of modeled parameters.

Table 3. Summary of Black-backed Woodpecker detections and posterior distributions of both fire-level (ω) and average point-level (ψ) predictions of occupancy probability for all fire areas surveyed during 2009 - 2012.

Fire name	2009 Detects. (# stns)	2010 Detects. (# stns)	2011 Detects. (# stns)	2012 Detects. (# stns)	ω_{2009}	ω_{2010}	ω_{2011}	ω_{2012}	ψ_{2009}	ψ_{2010}	ψ_{2011}	ψ_{2012}
Albanita	21 (1)	21 (0)	21 (0)	21 (6)	0.84	0.12	0.13	0.13	0.10	0.00	0.00	0.00
Angora	19 (13)	12 (7)	19 (13)	19 (13)	0.90	0.89	0.87	0.87	0.78	0.61	0.73	0.73
Antelope Complex	21 (9)	21 (2)	21 (6)	21 (8)	0.90	0.89	0.86	0.86	0.62	0.23	0.41	0.41
Azusa	8 (0)	-	-	-	0.12	-	-	-	0.00	-	-	-
Bassetts	18 (7)	18 (7)	-	19 (5)	0.89	0.88	-	0.18	0.48	0.44	-	0.00
Belden	-	13 (0)	13 (0)	13 (0)	-	0.61	0.18	0.11	-	0.00	0.00	0.00
Bell	20 (0)	20 (0)	20 (0)	-	0.11	0.10	0.11	-	0.00	0.00	0.00	-
Bell West	21 (1)	-	-	-	0.77	-	-	-	0.15	-	-	-
Birch	19 (0)	-	-	-	0.13	-	-	-	0.00	-	-	-
Blue	20 (5)	20 (5)	20 (5)	-	0.81	0.78	0.79	-	0.59	0.32	0.34	-
Boulder Complex	20 (9)	20 (1)	-	-	0.88	0.88	-	-	0.54	0.09	-	-
Broder Beck	-	20 (7)	20 (0)	20 (2)	-	0.87	0.16	0.79	-	0.41	0.00	0.34
Brown	-	20 (7)	20 (14)	20 (10)	-	0.92	0.88	0.16	-	0.37	0.75	0.00
Bucks	20 (0)	-	-	-	0.09	-	-	-	0.00	-	-	-
Clover	-	20 (7)	20 (0)	20 (1)	-	0.91	0.19	0.88	-	0.42	0.00	0.75
Cold	-	-	-	19 (11)	-	-	-	0.19	-	-	-	0.00
Comb	-	-	-	20 (0)	-	-	-	0.81	-	-	-	0.36
Cone	21 (5)	-	21 (6)	-	0.82	-	0.81	-	0.47	-	0.36	-
Cooney	-	-	-	20 (1)	-	-	-	0.14	-	-	-	0.00
Corral	-	-	-	20 (10)	-	-	-	0.16	-	-	-	0.00
Cougar	-	-	-	20 (13)	-	-	-	0.79	-	-	-	0.39
Crag 04	19 (4)	-	18 (0)	19 (1)	0.86	-	0.14	0.88	0.29	-	0.00	0.25
Crag 05	21 (0)	20 (0)	21 (0)	21 (0)	0.19	0.16	0.16	0.15	0.00	0.00	0.00	0.00
Crater	20 (8)	20 (3)	20 (7)	-	0.81	0.77	0.79	-	0.48	0.20	0.39	-
Cub	-	20 (3)	20 (3)	15 (1)	-	0.91	0.88	0.19	-	0.17	0.25	0.00
Deep	11 (0)	11 (0)	11 (0)	11 (0)	0.49	0.30	0.15	0.86	0.00	0.00	0.00	0.53
Devils Gap	20 (0)	-	-	-	0.09	-	-	-	0.00	-	-	-

Fire name	2009 Detects. (# stns)	2010 Detects. (# stns)	2011 Detects. (# stns)	2012 Detects. (# stns)	ω_{2009}	ω_{2010}	ω_{2011}	ω_{2012}	ψ_{2009}	ψ_{2010}	ψ_{2011}	ψ_{2012}
Dexter	16 (6)	16 (1)	-	16 (7)	0.84	0.82	-	0.18	0.53	0.19	-	0.00
Fall	10 (0)	10 (1)	10 (0)	10 (1)	0.42	0.91	0.19	0.14	0.02	0.16	0.00	0.00
Fletcher	19 (15)	17 (5)	19 (8)	20 (10)	0.90	0.90	0.86	0.18	0.90	0.40	0.53	0.00
Fox	-	-	18 (0)	-	-	-	0.18	-	-	-	0.00	-
Freds	20 (0)	-	19 (0)	20 (0)	0.17	-	0.14	0.11	0.00	-	0.00	0.00
Frey	-	20 (0)	18 (0)	-	-	0.49	0.18	-	-	0.00	0.00	-
Gap	-	20 (0)	19 (0)	-	-	0.10	0.11	-	-	0.00	0.00	-
Gondola	12 (6)	12 (4)	-	12 (2)	0.83	0.80	-	0.88	0.74	0.43	-	0.31
Government	19 (1)	19 (3)	19 (4)	-	0.91	0.91	0.88	-	0.10	0.20	0.31	-
granite	-	20 (6)	20 (10)	-	-	0.92	0.88	-	-	0.37	0.53	-
Grease	-	-	-	17 (0)	-	-	-	0.88	-	-	-	0.53
Harding	21 (7)	21 (2)	21 (0)	20 (0)	0.87	0.86	0.14	0.14	0.41	0.14	0.00	0.00
High	-	19 (1)	19 (5)	19 (11)	-	0.87	0.86	0.86	-	0.07	0.36	0.36
Highway	-	-	20 (0)	-	-	-	0.11	-	-	-	0.00	-
Hiram	10 (0)	-	-	-	0.10	-	-	-	0.00	-	-	-
Hooker	20 (0)	16 (0)	20 (0)	20 (0)	0.14	0.12	0.13	0.11	0.00	0.00	0.00	0.00
Horton 2	20 (7)	-	-	-	0.77	-	-	-	0.51	-	-	-
Inyo Complex	16 (0)	-	-	-	0.26	-	-	-	0.00	-	-	-
Kibbie	21 (6)	-	21 (3)	21 (5)	0.85	-	0.81	0.13	0.33	-	0.21	0.00
Knight	-	19 (0)	19 (0)	19 (0)	-	0.61	0.20	0.81	-	0.01	0.00	0.21
Lion	-	20 (7)	20 (2)	20 (6)	-	0.92	0.88	0.88	-	0.41	0.15	0.15
Lion 11	-	-	-	20 (4)	-	-	-	0.20	-	-	-	0.00
Lookout	21 (0)	-	-	-	0.10	-	-	-	0.00	-	-	-
Manter	21 (0)	20 (0)	-	-	0.14	0.08	-	-	0.00	0.00	-	-
Mclaughlin	-	13 (0)	13 (1)	-	-	0.10	0.79	-	-	0.00	0.13	-
McNally	19 (0)	17 (0)	16 (0)	17 (0)	0.35	0.23	0.12	0.79	0.00	0.00	0.00	0.13
Moonlight	20 (11)	20 (5)	20 (11)	20 (11)	0.90	0.90	0.86	0.12	0.61	0.28	0.61	0.00
Motor	-	-	-	24 (0)	-	-	-	0.86	-	-	-	0.61
Mountain	-	12 (1)	12 (3)	9 (4)	-	0.82	0.82	0.82	-	0.21	0.32	0.32

Fire name	2009 Detects. (# stns)	2010 Detects. (# stns)	2011 Detects. (# stns)	2012 Detects. (# stns)	ω_{2009}	ω_{2010}	ω_{2011}	ω_{2012}	ψ_{2009}	ψ_{2010}	ψ_{2011}	ψ_{2012}
Mud	21 (10)	20 (12)	21 (8)	21 (8)	0.85	0.81	0.82	0.82	0.54	0.65	0.44	0.44
North Fork	20 (0)	13 (0)	8 (0)	-	0.25	0.17	0.12	-	0.00	0.00	0.00	-
Oliver	-	-	17 (6)	-	-	-	0.87	-	-	-	0.43	-
Onion 2	-	20 (0)	20 (0)	20 (1)	-	0.30	0.18	0.12	-	0.00	0.00	0.00
Peavine	16 (0)	-	-	-	0.54	-	-	-	0.01	-	-	-
Peterson Complex	20 (9)	20 (7)	20 (14)	20 (3)	0.92	0.91	0.87	0.87	0.51	0.37	0.74	0.43
Pidgen	18 (0)	-	-	-	0.09	-	-	-	0.00	-	-	-
Pit	-	-	-	20 (2)	-	-	-	0.18	-	-	-	0.00
Piute 08	20 (0)	19 (0)	-	-	0.37	0.23	-	-	0.00	0.00	-	-
Plum	12 (0)	12 (0)	12 (0)	13 (0)	0.29	0.22	0.12	0.87	0.00	0.00	0.00	0.74
Power	20 (1)	20 (0)	20 (0)	20 (2)	0.86	0.18	0.13	0.12	0.10	0.00	0.00	0.00
Rich	21 (1)	21 (1)	-	21 (6)	0.91	0.91	-	0.13	0.12	0.08	-	0.00
Sawmill 00	5 (0)	-	-	-	0.17	-	-	-	0.01	-	-	-
Sawmill 06	-	-	19 (0)	-	-	-	0.16	-	-	-	0.00	-
Scotch	21 (3)	21 (0)	-	21 (1)	0.91	0.29	-	0.16	0.22	0.01	-	0.00
Sheep	-	-	-	20 (1)	-	-	-	0.88	-	-	-	0.68
Shotgun	-	-	-	16 (3)	-	-	-	0.79	-	-	-	0.18
Showers	9 (3)	9 (6)	-	8 (4)	0.82	0.79	-	0.11	0.52	0.72	-	0.00
Silver	-	-	11 (7)	11 (6)	-	-	0.88	0.88	-	-	0.68	0.29
Star	-	20 (6)	20 (1)	-	-	0.77	0.79	-	-	0.35	0.18	-
Storrie	15 (4)	-	-	-	0.80	-	-	-	0.48	-	-	-
Straylor	-	-	-	20 (1)	-	-	-	0.14	-	-	-	0.00
Stream	20 (0)	20 (0)	15 (0)	-	0.11	0.09	0.11	-	0.00	0.00	0.00	-
Sugar Loaf	-	21 (3)	21 (2)	21 (0)	-	0.92	0.88	0.86	-	0.17	0.29	0.17
Summit	-	-	16 (0)	-	-	-	0.14	-	-	-	0.00	-
Tamarack	-	-	-	20 (3)	-	-	-	0.12	-	-	-	0.00
Tehipite	-	-	-	21 (9)	-	-	-	0.82	-	-	-	0.41
Treasure	10 (2)	10 (4)	-	-	0.80	0.77	-	-	0.29	0.42	-	-
Vista	19 (9)	19 (8)	19 (2)	19 (5)	0.90	0.90	0.86	-	0.52	0.50	0.17	-

Fire name	2009 Detects. (# stns)	2010 Detects. (# stns)	2011 Detects. (# stns)	2012 Detects. (# stns)	ω_{2009}	ω_{2010}	ω_{2011}	ω_{2012}	ψ_{2009}	ψ_{2010}	ψ_{2011}	ψ_{2012}
Whit	20 (6)	-	20 (7)	19 (9)	0.84	-	0.82	-	0.36	-	0.41	-
White	8 (0)	8 (0)	8 (0)	-	0.23	0.20	0.12	-	0.00	0.01	0.00	-
Total	899 (169)	860 (132)	895 (148)	953 (207)	0.6 (0.55 - 0.67)	0.65 (0.59 - 0.71)	0.48 (0.48 - 0.5)	0.78 (0.75 - 0.83)	0.25 (0.22 - 0.31)	0.19 (0.17 - 0.21)	0.21 (0.18 - 0.24)	0.24 (0.23 - 0.26)

Models of annual occupancy show changes in the total estimated proportion of (sampled) fire areas being occupied by at least one Black-backed Woodpecker in different years (Table 3). The proportion of occupied fire areas (ω) in 2009 and 2010 appears to have been relatively stable (0.60 and 0.65, respectively, with overlapping confidence intervals), while the proportion in 2011 was significantly lower (0.48). This proportion then increased significantly in 2012 (0.78, 95% CI: 0.75 – 0.83). Given that different fires were sampled in different years, the interpretation of these differences is difficult. However, there were six fires (Table 3) where Black-backed Woodpeckers were not detected in 2011 but were detected in 2012, compared to only one fire where detections occurred in 2011 but not 2012. While these metrics suggest real increases in population size between 2011 and 2012, actual changes in colonization or extinction are best understood through dynamic occupancy models (see next section).

We compared modeled covariate relationships with occupancy and detectability for each of the four annual occupancy models (Table 4). Covariate signs showed general consistency across years, although 2012 showed slightly different relationships and covariate strengths compared to previous years. Although fire age was a significant effect in the 2009 and 2010 models, the effect has been growing weaker, and was not significant in 2011 or 2012 models. Burn severity was only significant for the 2009 model, and in 2012, the mean relationship was barely positive. The relationship between occupancy and pre-fire canopy cover was positively significant in 2010 (i.e., occupancy increases with pre-fire canopy cover), but was negative and significant in 2012 (the relationship was positive but not significant in 2009 and 2011). The relationship of occupancy with snag density remained positive in 2012 and was the strongest of the four years. Of the factors affecting duration, survey type (i.e., passive versus broadcast) is the only covariate which has remained significant across all 4 years (broadcast has a higher detection rate than passive).

Table 4. Posterior summaries (means and 95% credible intervals) for intercepts and regression coefficients for single-year occupancy models as applied to 2009-2012 survey data.

Parameter	Year			
Fire level occupancy probability	2009	2010	2011	2012
σ_f (variance of random fire effect)	6.5 (0.93 - 9.87)	6.34 (1.05 - 9.85)	6.2 (0.57 - 9.86)	6.4 (0.89 – 9.86)
γ_1 (fire age)	-2.76 (-6.58 - -0.14)	-3.23 (-7.42 - -0.39)	-1.83 (-5.15 - 0.44)	-0.49 (-3.77 – 2.49)
Point-level occupancy probability				
β_0	-1.01 (-1.37 - -0.61)	-1.17 (-1.47 - -0.86)	-0.45 (-0.76 - -0.11)	-0.97 (-1.19 - -0.77)
β_1 (latitude)	0.54 (0.17 - 1.01)	-0.26 (-0.53 – 0.00)	0.22 (-0.06 - 0.52)	0.53 (0.34 – 0.73)
β_2 (elevation)	1.20 (0.70 - 1.91)	0.81 (0.45 - 1.16)	-0.07 (-0.37 - 0.24)	0.53 (0.27 – 0.80)
β_3 (snag density)	0.08 (-0.18 - 0.32)	0.29 (0.00 - 0.60)	0.10 (-0.15 - 0.36)	0.36 (0.18 – 0.54)
β_4 (burn severity)	0.37 (0.06 - 0.72)	0.21 (-0.05 - 0.47)	0.20 (-0.09 - 0.49)	0.03 (-0.18 – 0.22)
β_5 (pre-fire canopy cover)	0.06 (-0.22 - 0.33)	0.35 (0.06 - 0.63)	0.22 (-0.03 - 0.48)	-0.21 (-0.41 – -0.01)
Detection probability				
α_0	-3.45 (-4.41 - -2.65)	-1.57 (-1.89 - -1.25)	-1.2 (-1.58 - -0.83)	-0.94 (-1.24 - -0.63)
α_1 (interval duration)	1.94 (1.11 - 2.91)	0.72 (0.14 - 1.31)	0.09 (-0.51 - 0.68)	0.25 (-0.25 – 0.75)
α_2 (survey type)	2.83 (2.03 - 3.77)	1.05 (0.65 - 1.47)	0.67 (0.22 - 1.12)	0.92 (0.53 – 1.30)
α_3 (day of year)	-0.24 (-0.54 - 0.06)	-0.16 (-0.41 - 0.08)	0.01 (-0.21 - 0.22)	0.07 (-0.11 – 0.26)

Analysis of Dynamic Occupancy

Of the 1599 survey points, 979 (61%) were surveyed in more than one year and 262 (16%) were surveyed in all four years. Of those points that were surveyed in more than one year, 202 (13%) showed apparent colonizations (i.e., not detected in one year, detected in subsequent) and 225 (14%) showed apparent extinctions. This degree of apparent occurrence change (44%) at revisited points facilitated the building of dynamic occupancy models focused on the estimation of point-specific colonization and extinction probabilities.

The analysis of three years of data (Siegel et al. 2012) exploring 56 model parameterizations of detectability and initial occupancy resulted in strong support for the saturated model, which included survey duration, survey type, and day of year as covariates of detectability, and elevation, elevation^2, and latitude as covariates of initial occupancy. As adding additional data is unlikely to decrease the number of variables selected, and since previous analyses indicates all of these factors to be important for detection and occupancy (Saracco et al., 2011), the saturated model was used for parameterization of detection and occupancy with 2009-2012 data, without additional testing.

Model support for colonization and extinction models was broadly distributed across many similar candidate models (Table 5). Nine models were within 2 AIC units of each other, an index often used to delineate models with "substantial support" (Burnham and Anderson 2002). These 9 models, together, comprised 37% of the total AIC model weight. The covariates selected were very similar to those selected previously using only 3 years of data (Siegel et al. 2012). The number of models within 2 AIC units was reduced from 12 to 9 by adding data for 2012, illustrating how additional years of data increase the ability to discriminate among multiple competing models.

Table 5. Top models ($\Delta_i < 2$) comparing different combinations of colonization and extinction covariates for point-level analysis.

Colonization covariates	Extinction covariates	K	AIC	Δ_i	w_i
Snag density + fire age	Burn severity + canopy cover	14	2227	0.00	0.07
Snag density + fire age	-	12	2228	0.44	0.06
Snag density + fire age	Burn severity	13	2228	0.57	0.05
Snag density + fire age	Canopy cover	13	2228	0.59	0.05
Snag density + fire age	Burn severity + canopy cover + fire age	15	2229	1.94	0.03
Snag density + fire age + burn severity	Burn severity + canopy cover	15	2229	1.95	0.03
Snag density + fire age	Burn severity + canopy cover + snag density	15	2229	1.95	0.03
Snag density + fire age + canopy cover	-	13	2229	1.97	0.03
Snag density + fire age + canopy cover	Burn severity + canopy cover	15	2229	2.00	0.03

Although there is no single clear "top model" for colonization and extinction models, there is general consistency in support for certain variables. For instance, all top models within 2 AIC units included both snag density and fire age as colonization covariates, while there was greater uncertainty with regard to important variables for extinction covariates (Table 5). Indeed, the 2nd and 8th ranked extinction models were "null" models where extinction was essentially a random process with a fixed probability.

The differences between colonization and extinction are clearly shown by the cumulative AIC weight ("relative importance" or $w_+(j)$; Burnham and Anderson 2002) in support of different covariates for colonization and extinction (Table 6). Both snag density and fire age have nearly full, universal support as covariates of colonization, while burn severity and pre-fire canopy cover have middle support (> 0.5). There is essentially no support (< 0.01) for models that had colonization as a random process at a fixed probability. In comparison, the cumulative weights for covariates of extinction showed much more widespread, ambiguous support. These data show that colonization dynamics are strongly predicted by snag density and fire age, while extinction dynamics are moderately predicted by burn severity and pre-fire canopy cover. There is a non-zero probability (0.13) that extinction is a random occurrence.

Table 6. Cumulative AIC weights in support of individual covariates in compared models for both colonization and extinction probabilities.

Covariate	Colonization relative importance score	Extinction relative importance score
Null (random)	0.00	0.13
Snag density	0.94	0.29
Fire age	0.96	0.29
Burn severity	0.29	0.53
Pre-fire canopy cover	0.30	0.51

Compared to analyses with only three years of data (Siegel et al., 2012), the addition of data from 2012 improved support for covariates of colonization and extinction. Cumulative AIC weights for fire age and burn severity as covariates of colonization improved by 5% and 6%, respectively. Cumulative AIC weight for burn severity as covariate of extinction increased by 12%, while cumulative AIC weight for fire age and pre-fire canopy cover as extinction covariates decreased by 13% and 3%, respectively. The large decrease in support for fire age as a covariate of extinction coupled with the increase in support for fire age as a covariate of colonization suggests that as more fires are sampled over an increasing number of years the importance of fire age to extinction lowers. These relationships will likely continue to clarify with increasing years of sampling.

Of critical interest is the sign and magnitude of covariate relationships to probabilities of colonization and extinction (Table 7). Based on the top AIC-ranked model (Table 5), while average point-level probability of colonization (that is, the probability of a point being unoccupied in one post-fire year and then being occupied in the next year) is low (7.8%), the probability of colonization significantly increases with snag density but decreases with fire age. In comparison, the average probability of extinction is high (67%) and decreases with increased burn severity and increased pre-fire canopy cover. In the top model, however, these covariate effects of extinction were not significant (Table 7).

Table 7. Covariate parameter estimates, standard errors, and significance for the best-supported colonization-extinction model at point-level.

Parameter	Covariate	Estimate	Std. Error	*P*
Detectability	Intercept	-0.80	0.11	< 0.001
-	Interval length	0.79	0.17	< 0.001
-	Survey type	0.10	0.19	0.580
-	Day of year	-0.18	0.09	0.042
Initial occupancy	Intercept	-2.67	0.24	< 0.001
-	Elevation	1.90	0.60	0.001
-	Elevation^2	-1.02	0.49	0.040
-	Latitude	0.29	0.17	0.082
Colonization	Intercept	-2.47	0.16	< 0.001
-	Snag density	0.27	0.10	0.005
-	Fire age	-0.45	0.15	0.002
Extinction	Intercept	0.70	0.29	0.017
-	Burn severity	-0.37	0.23	0.116
-	Pre-fire canopy cover	-0.42	0.27	0.121

Over the range of values for which snag density and fire age were observed in the Sierra Nevada, the probability of colonization (of an unoccupied survey point at least one year post-fire) only ever approached 50% for points less than or equal to 4-years post-fire and only at the points with the highest snag densities (~ >200 snags per ha) (Figure 7). On average, after 3-years post-fire, the probability of an unoccupied point being colonized by Black-backed Woodpeckers in any subsequent year drops below 10%. However, cumulatively, the probability that an average point (snag density ~30 snags/ha) that is unoccupied at 1-year post fire will become colonized in any year over the next 9 years is around 50% (Figure 8). This assumes that the density of snags at a point is constant and does not change over time – an assumption we know is invalid, as snags may increase in the first few years as trees continue to die but eventually will decrease with time as they decay and fall. Consequently, the true probability that a point unoccupied in year *i* will become colonized at some time between year *i*+1 and 10 will be lower than modeled here.

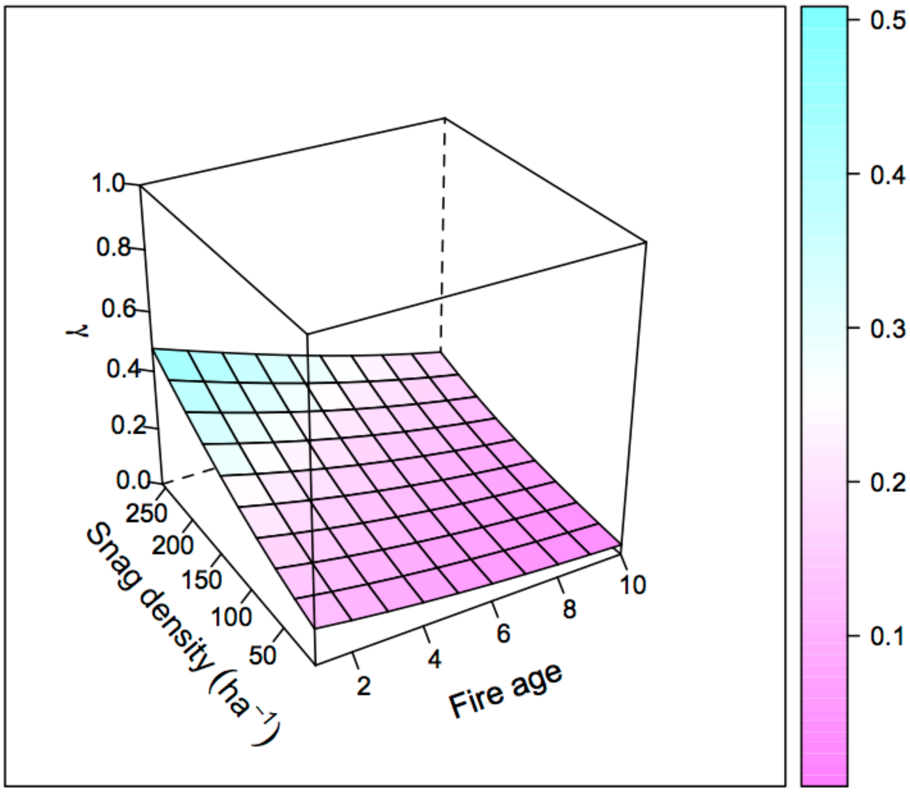

Figure 7. The modeled relationship between the probability of colonization (γ), the snag density at a point, and the number of years post-fire.

While colonization probability decreases with time, the best supported model indicates that extinction probability is time-insensitive (although there is marginal support for extinction varying with fire age across all compared models; Table 6) but decreases with higher levels of burn severity and pre-fire canopy cover. In other words, at points where pre-fire forest conditions were denser or where the fire burned more severely, Black-backed Woodpeckers were more likely to persist longer post-fire. Although pre-fire canopy cover and burn severity interact to result in snag density, the strength of these individual relationships appears stronger than the direct relationship between extinction and snag density (Table 6).

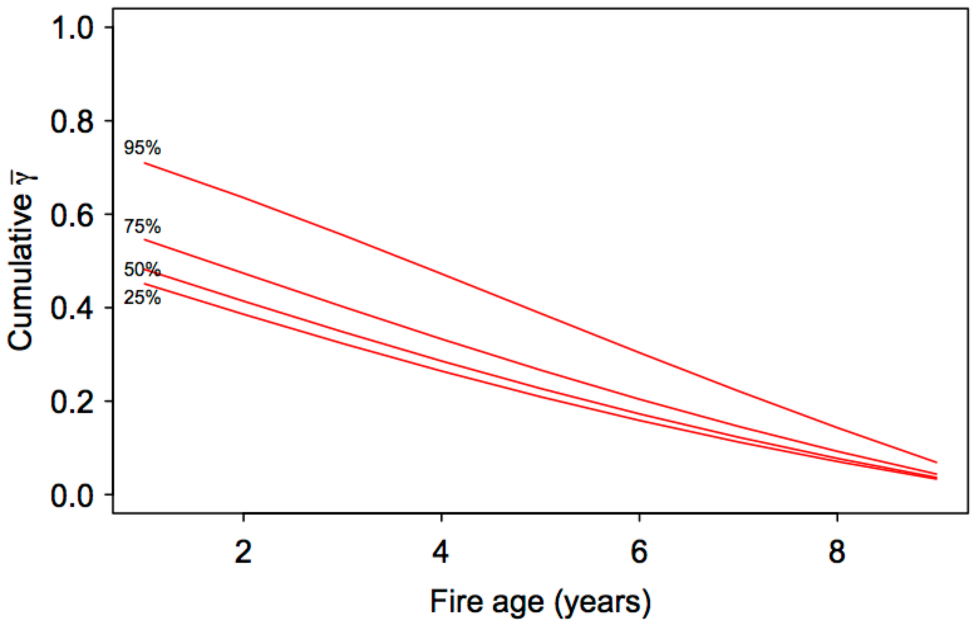

Figure 8. The modeled relationship between fire age and the average cumulative probability of colonization for four levels of snag density. Given an unoccupied point *i*-years post-fire (i.e., x-axis: fire age), the y-axis is the probability that that point will be colonized in any subsequent year, from *i* +1 to 10. Chosen snag densities represent the 5th and 25th (3.8 snag/ha), 50th (16.5 snag/ha), 75th (42 snag/ha), and 95th (106 snag/ha) percentiles of snag densities observed at plots. Graph assumes that snag densities are constant over time.

Fire-level Dynamic Occupancy

Over the four years of sampling, a total 87 fires have been surveyed for Black-backed Woodpeckers, of which 54 (62%) have had woodpecker detections in one or more years. The factors that result in colonizations or extinctions at fires may be different than the factors that cause colonizations or extinctions at individual survey points within fires. To explore this, we conducted a separate dynamic occupancy modeling analysis – at the fire level – that sought to understand whether colonization or extinction probability differed by total area extent of the fire, the survey year, and fire age.

To parameterize the models, a two-stage analysis was conducted, first fitting covariates of detection and initial occupancy, and second fitting covariates of colonization and extinction. Identical covariates were tested for initial occupancy and detection, comprising 56 models. Of these models, the top model (Table 8), with 36% of the AIC weight, included elevation and latitude as covariates of initial occupancy, and survey effort and survey type as covariates of detection. This parameterization is nearly the same as that selected for survey point-level occupancy (it excludes the quadratic effect of elevation).

Table 8. Top models ($\Delta_i < 2$) comparing different combinations of initial occupancy and detection covariates for fire-level analysis.

Initial occupancy covariates	Detection covariates	K	AIC	Δ_i	w_i
Elevation + latitude	Effort + survey type	8	824.4	0.00	0.36
Elevation + latitude	Effort + survey type + Julian day	9	824.8	0.43	0.29
Elevation + elevation^2 + latitude	Effort + survey type	9	825.7	1.34	0.18
Elevation + elevation^2 + latitude	Effort + survey type + Julian day	10	826.0	1.67	0.15

In the second stage of the analysis, 36 models were tested with differing parameterizations of colonization and extinction probability (Table 9). The top selected model included fire age as a covariate of colonization, and year as a covariate of extinction. Area (ha) of fire showed poor model support across top models (Table 9).

Table 9. Top models ($\Delta_i < 2$) comparing different combinations of colonization and extinction covariates for fire-level analysis.

Colonization covariates	Extinction covariates	K	AIC	Δ_i	w_i
Fire age	Year	11	820.7	0.00	0.13
Year	Year	12	820.9	0.21	0.12
Fire age	Year + area	12	822.3	1.52	0.06
-	Year	10	822.3	1.60	0.06
Year + area	Year	13	822.4	1.67	0.06
Fire age + area	Year	12	822.4	1.67	0.06
Year	Year + area	13	822.5	1.73	0.06
Fire age	-	9	822.6	1.91	0.05

Exploration of modeled parameters for this top model (Table 10) show that colonization probability decreases with fire age, and that the probability of extinction in years 2010 and 2011 was higher than in 2009. The effect of year on extinction, however, was greatly uncertain (Table 10), even though year was supported as a covariate of extinction in 7 of the 8 models within 2 AIC units of the top model (Table 9). Taken together, it remains uncertain whether the probability of Black-backed Woodpecker extinction at fires varied by year, occurred at random with a fixed probability, or is a function of some factor not explored in this analysis.

Table 10. Covariate parameter estimates, standard errors, and significance for the best-supported colonization-extinction model at fire-level.

Parameter	Covariate	Estimate	Std. Error	*P*
Detectability	Intercept	-0.34	0.13	0.008
-	Interval length	0.76	0.23	0.001
-	Survey type	1.71	0.25	0.000
Initial occupancy	Intercept	-0.56	0.44	0.198
-	Elevation	2.44	0.90	0.006
-	Latitude	2.36	0.85	0.005
Colonization	Intercept	-1.53	0.38	0.000
-	Fire age	-0.74	0.41	0.069
Extinction	Intercept	-8.88	24.06	0.712
-	Year (2010)	7.76	24.07	0.747
-	Year (2011)	6.54	24.08	0.786

Analysis of Multispecies Occupancy

A total of 150 bird species have been detected during passive bird surveys at Black-backed Woodpecker points (Appendix I). In 2012, five new species were detected on point counts that had not previously been detected: Peregrine Falcon, American Dipper, Northern Goshawk, Nuttall's Woodpecker, and Spotted Owl. Our goals for the present analysis were to assess how species community structure changed over time in the 10 years post-fire and to assess which species were most strongly associated with different fire ages.

Nonmetric Multidimensional Scaling was conducted on bird abundances estimated from 202 yearly samples of 87 fires (Figure 9). Ordination of mean abundance yielded a 2-dimensional solution (stress = 22.4). Six environmental factors were correlated with both ordination axes, including fire age, fire-level means of live tree density, snag density, pre-fire canopy cover, and burn severity, as well as fire-level standard deviation of burn severity (to account for intra-fire burn severity heterogeneity at survey points). All six factors were significantly correlated given 1000 permutations (all $p < 0.05$; Figure 9A). To further explore the effect of fire age, 95% confidence ellipses and centroids were plotted for communities of each fire age (Figure 9B). As forests aged from 1-10 years post-fire, communities showed a clear linear trajectory (on both NMDS axis 1 and NMDS axis 2) for years 1-5. After year 5, however, the linear trajectory ends, and centroids are clustered together (Figure 9B). This suggests that the greatest changes in bird communities occurred yearly in the first 5 years post-fire, but that after this time, the bird communities showed relative stability. It should be noted there is great heterogeneity in community structure within forests of a given time-since-fire. Any single community 1-year post-fire could show greater similarity to a community 10-years post-fire than to other communities 1-year post-fire, as evidenced by overlapping confidence ellipses in Figure 9B. On average, however, communities show linear dissimilarity trends in the first 5 years post-fire.

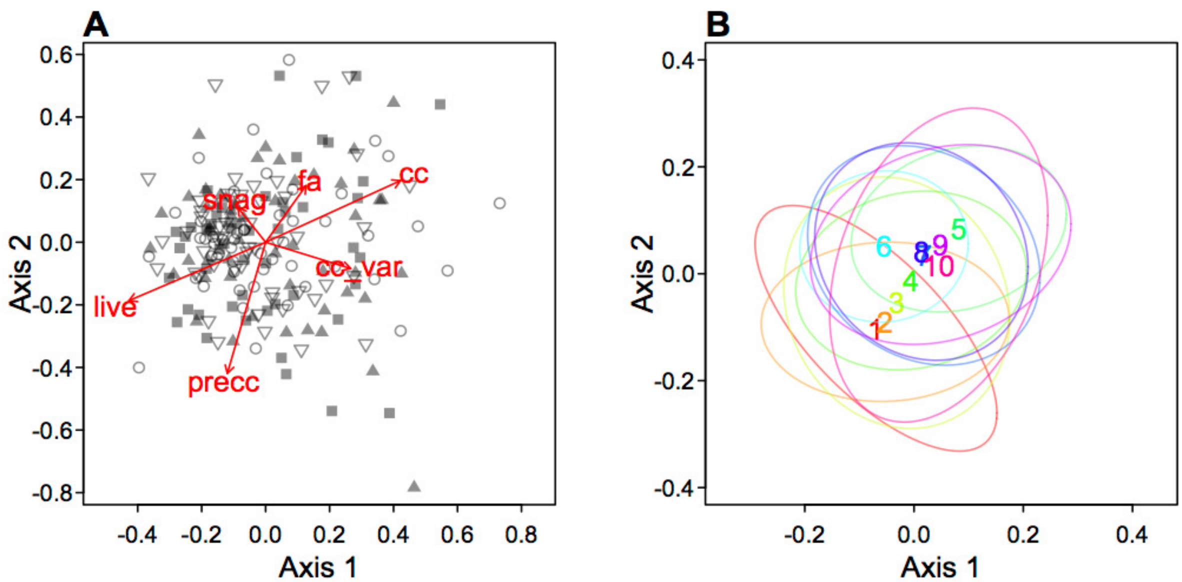

Figure 9. Ordination plots from Nonmetric Multidimensional Scaling on bird communities at 202 yearly samples of 87 fires. (A) Ordination of yearly samples (open circle = 2009, open triangle = 2010, closed square = 2011, closed triangle = 2012) with significantly correlated environmental vectors overlaid (live = mean density of live trees; snag = mean density of snags; fa = fire age; cc = mean burn severity; cc_var = standard deviation of burn severity at points within fire; precc = mean pre-fire canopy cover). (B) 95% confidence ellipses and centroids (identified by numbers) of communities of a given fire age. Centroid numbers identify the age of the forest post-burn, and show a linear trend through ordination space for years 1-5.

Indicator species analysis allows one to quantify the degree to which a species is associated with a given set of environmental conditions.(in this case, years since fire). Values range from 0 to 100, with higher numbers indicating a tighter affinity to the environmental conditions considered. Indicator species analysis identified 11 bird species that significantly indicated for 4 of the 10 post-fire years (Table 11). Generally, indicator scores were low (max = 16, mean = 3.5), but this is dependent on the number of classes and the differences between them. As each post-fire year was treated as a separate class, few species strongly indicated fidelity to any single post-fire year. Higher indicator values would have been calculated if post-fire years were clustered into fewer groups.

Of the 126 species analyzed, at least 8 species had a maximum indicator score for every post-fire year. The four post-fire years with significant indicators were years 2, 4, 5, and 10 (Table 11). The spread of these values demonstrates the post-fire years in which ‘unique’ bird communities occur. Years in-between represent transition zones, in other words: years 1-2, 2-4, 4-5, and 5-10 can be considered transitional but distinct community assemblages. This finding agrees with the previous ordination analysis, which found a linearly changing community for years 1-5, but little change (yet high variability) from years 5-10.

Black-backed Woodpecker was identified as a significant indicator for forests that were 4-years post-fire. Other species that were significant for 4-years post-fire were Evening Grosbeak and Hammond’s Flycatcher. Black-backed Woodpecker also showed high indicator values for 5-years post-fire, but very low values for years 7-10.

The indicator species identified illustrate the transitions that occur in the first 10 years post-fire. Early post-fire indicators were Townsend’s Solitaire and Western Tanager. Neither are considered burned-forest specialists, but may take advantages of openings within intact conifer forests. As many burned or dying trees retain needles for the first 2 years post-fire, some “green forest” species are typical of the early post-fire years. By years 4-5, however, the bird community has transitioned to one dominated by open forest, snag-associated, or edge species. Black-backed Woodpecker is a strong indicator, but so is Chipping Sparrow and Rock Wren (both indicators for post-fire year 5). Other species like Western and Mountain Bluebirds and Lazuli Buntings peak as indicators during this period (but are not significantly associated with a single post-fire year). Finally, by year 10 many fires exhibit robust shrub growth and many shrub-dominant bird species become dominant. Of the three significant indicators for year 10, Yellow Warbler and Orange-crowned Warbler are both species that require dense shrub or chaparral for breeding, and the third species, Tree Swallow, is a secondary cavity nester. Other species that reach maximum indicator values in year 10 are also characteristic of a shrub-dominated ecosystem: Nashville and MacGillivray's Warblers, California and Spotted Towhees, Blue-gray Gnatcatcher, Wrentit, and Western Scrub-Jay.

Table 11. Indicator species analysis of bird species found in burned forests, sorted by P-value and year within which each species achieved its maximum indicator score (species with significant scores are highlighted in bold; indicator values range 0-100).

Species Name	Percent Indicator Value										P-value
	Year 1	Year 2	Year 3	Year 4	Year 5	Year 6	Year 7	Year 8	Year 9	Year 10	
Purple Finch	9	1	1	2	3	1	0	8	0	0	0.092
Black Phoebe	6	1	-	-	-	-	-	-	1	1	0.151
Anna's Hummingbird	8	4	2	0	-	1	4	2	1	0	0.163
Common Poorwill	4	-	-	-	-	-	-	-	2	-	0.243
Lawrence's Goldfinch	4	2	-	-	-	-	-	-	-	-	0.249
Dusky Flycatcher	11	7	6	6	7	8	3	5	5	5	0.333
Northern Goshawk	4	-	-	2	-	-	-	-	-	-	0.364
Ruby-crowned Kinglet	4	1	1	-	-	-	-	1	-	-	0.425
White-throated Swift	3	1	-	-	-	-	-	1	-	-	0.471
Lark Sparrow	3	-	1	-	-	-	1	1	-	1	0.621
Black-headed Grosbeak	7	6	7	7	5	1	4	4	1	5	0.869
Townsend's Solitaire	6	**16**	2	7	7	7	2	5	3	2	0.011
Western Tanager	13	**14**	12	12	6	10	6	6	8	7	0.025
Band-tailed Pigeon	-	7	2	2	-	-	-	-	-	0	0.078
Red-breasted Nuthatch	12	13	9	9	4	8	4	8	4	5	0.106
Hermit Warbler	0	10	8	7	0	2	0	1	0	1	0.113
Pine Siskin	4	9	1	4	1	3	0	0	0	1	0.122
Black-throated Gray Warbler	2	7	4	2	-	-	0	0	2	-	0.187
Downy Woodpecker	2	6	-	0	-	-	3	-	2	-	0.198
Cassin's Vireo	5	10	8	8	0	3	2	3	2	4	0.285
Mountain Quail	6	10	2	2	7	7	4	4	4	4	0.308
Calliope Hummingbird	1	4	-	-	1	3	0	-	0	0	0.396
Rufous Hummingbird	-	4	-	0	3	-	1	-	0	-	0.465
Mourning Dove	4	7	2	4	5	1	3	1	2	1	0.549
American Crow	-	4	-	-	-	-	-	-	-	-	0.866
Gray Jay	-	4	-	-	-	-	-	-	-	-	0.871

Species Name	Percent Indicator Value										P-value
	Year 1	Year 2	Year 3	Year 4	Year 5	Year 6	Year 7	Year 8	Year 9	Year 10	
Pacific Wren	-	-	3	2	-	-	-	-	1	-	0.560
Pacific-slope Flycatcher	2	-	4	3	1	-	-	0	0	1	0.581
Hermit Thrush	3	3	4	4	-	0	0	0	-	1	0.618
Warbling Vireo	3	3	8	7	1	5	2	6	5	5	0.668
American Dipper	-	-	4	-	-	-	-	-	-	-	0.743
Peregrine Falcon	-	-	4	-	-	-	-	-	-	-	0.747
Hutton's Vireo	2	0	2	0	-	-	-	-	0	2	0.756
Pileated Woodpecker	1	0	3	3	1	1	0	1	-	0	0.883
Wilson's Warbler	-	1	2	2	2	1	2	0	-	1	0.951
American Goldfinch	-	1	1	-	-	-	-	1	1	-	0.993
Evening Grosbeak	0	1	3	**14**	0	1	-	0	0	3	0.014
Black-backed Woodpecker	3	3	2	**13**	7	4	0	2	2	0	0.018
Hammond's Flycatcher	0	1	5	**6**	-	2	0	0	0	1	0.334
Steller's Jay	9	12	9	12	9	11	8	7	8	6	0.335
Brown-headed Cowbird	4	2	4	7	5	2	1	2	4	5	0.587
Bewick's Wren	1	-	1	3	-	1	2	1	0	-	0.695
Golden-crowned Kinglet	2	1	2	5	2	3	0	3	4	3	0.760
Nuttall's Woodpecker	-	-	-	4	-	-	-	-	-	-	0.779
Red-breasted Sapsucker	2	0	2	6	3	5	3	5	3	5	0.798
Townsend's Warbler	-	-	-	2	-	-	-	-	2	-	0.810
Sooty Grouse	1	0	1	2	-	1	0	1	1	1	0.963
Great Horned Owl	-	1	-	1	-	-	-	1	-	-	0.992
Rock Wren	1	1	1	4	**16**	4	3	1	2	1	0.008
Chipping Sparrow	5	5	6	9	**15**	6	5	3	6	4	0.037
Killdeer	-	1	-	-	**9**	-	-	-	1	-	0.041
Hairy Woodpecker	7	13	11	12	14	7	6	4	5	4	0.065
American Robin	9	10	9	11	13	10	6	9	7	6	0.117
Green-tailed Towhee	3	2	1	2	12	11	9	12	7	10	0.137
House Wren	1	2	4	6	12	4	8	9	7	10	0.158

Species Name	Percent Indicator Value										P-value
	Year 1	Year 2	Year 3	Year 4	Year 5	Year 6	Year 7	Year 8	Year 9	Year 10	
European Starling	-	0	0	1	6	-	3	1	1	0	0.167
Clark's Nutcracker	0	0	1	1	8	3	1	3	4	1	0.190
Western Bluebird	4	0	4	9	9	2	3	1	2	3	0.232
Red-winged Blackbird	-	-	0	0	5	-	0	2	1	0	0.273
Western Meadowlark	-	-	1	2	5	0	1	-	0	0	0.275
Black-billed Magpie	-	-	-	2	4	-	-	-	-	-	0.351
Lazuli Bunting	3	10	4	4	10	1	5	4	5	4	0.355
Canyon Wren	-	-	1	-	3	-	-	-	-	1	0.371
Brewer's Blackbird	-	1	2	5	6	1	4	1	0	3	0.437
Mountain Bluebird	0	1	3	6	9	6	2	5	4	7	0.468
Red-tailed Hawk	-	-	1	1	4	0	0	3	2	2	0.536
Turkey Vulture	-	-	-	-	3	-	-	-	1	2	0.555
Williamson's Sapsucker	-	0	1	0	4	1	2	0	3	0	0.557
Pygmy Nuthatch	0	0	0	2	6	4	3	1	4	5	0.625
Chestnut-backed Chickadee	2	-	-	-	3	-	2	-	-	-	0.654
Lewis's Woodpecker	0	1	2	2	3	-	1	1	-	0	0.846
Common Raven	2	3	2	3	5	2	1	1	4	1	0.861
White-crowned Sparrow	-	0	-	1	2	-	1	1	1	1	0.929
Brown Creeper	4	10	6	9	7	14	5	11	9	4	0.065
Yellow-rumped Warbler	10	7	9	8	5	14	7	5	9	2	0.074
Cassin's Finch	7	6	5	8	7	13	8	8	5	7	0.115
Northern Pygmy-Owl	-	0	0	2	2	7	-	-	0	-	0.121
Lincoln's Sparrow	1	1	1	0	1	7	2	5	0	0	0.195
Purple Martin	-	-	-	-	2	5	-	-	-	-	0.310
Sharp-shinned Hawk	-	-	-	2	-	4	-	-	-	-	0.379
Western Screech-Owl	-	-	2	-	-	4	-	-	-	-	0.401
Mountain Chickadee	9	9	7	11	10	12	9	10	10	8	0.405
Bald Eagle	-	1	1	-	-	3	-	-	-	-	0.499
Western Wood-Pewee	7	8	7	9	10	12	8	11	9	7	0.548

Species Name	Percent Indicator Value										P-value
	Year 1	Year 2	Year 3	Year 4	Year 5	Year 6	Year 7	Year 8	Year 9	Year 10	
Oak Titmouse	-	-	-	1	2	-	5	-	-	-	0.156
White-breasted Nuthatch	1	2	1	7	9	9	11	2	8	4	0.169
Ash-throated Flycatcher	1	-	-	-	1	-	5	1	-	5	0.209
Fox Sparrow	5	3	4	6	9	8	12	10	7	8	0.240
Western Kingbird	-	-	-	-	-	1	3	3	-	1	0.444
Lesser Goldfinch	5	3	1	4	5	-	5	1	0	1	0.710
Vesper Sparrow	-	-	0	1	1	1	2	1	1	1	0.866
Bushtit	1	0	-	-	-	1	2	1	1	1	0.970
Red Crossbill	2	-	1	2	2	0	-	5	0	2	0.527
Osprey	-	1	-	-	-	2	-	3	2	-	0.546
Northern Flicker	2	4	5	10	10	5	8	10	9	6	0.644
House Finch	1	1	-	1	1	1	2	4	2	1	0.791
Common Nighthawk	-	1	-	1	-	1	1	2	-	-	0.843
Song Sparrow	-	1	1	1	2	-	1	3	1	3	0.846
Dark-Eyed Junco	11	10	10	10	9	11	9	11	7	6	0.903
Olive-sided Flycatcher	7	5	4	7	5	7	6	8	8	5	0.980
Pinyon Jay	-	-	-	-	-	-	-	-	11	1	0.062
Gray Flycatcher	1	0	0	1	1	3	0	1	9	3	0.082
American Kestrel	1	1	0	0	2	1	0	-	6	-	0.242
White-headed Woodpecker	4	3	6	7	5	9	4	2	11	4	0.255
Sage Sparrow	-	-	-	2	-	-	-	1	4	-	0.289
Juniper Titmouse	-	-	-	-	-	4	-	-	4	-	0.292
Violet-green Swallow	0	0	1	-	2	-	0	3	5	2	0.328
Brewer's Sparrow	-	-	-	-	2	-	4	3	5	4	0.400
Black-throated Sparrow	1	2	-	-	1	-	-	-	2	-	0.740
Cliff Swallow	-	-	-	-	-	-	-	2	3	-	0.965
Black-chinned Sparrow	-	1	-	-	-	-	-	1	2	1	0.993
Common Yellowthroat	-	-	-	-	-	-	-	-	4	-	1.000
Yellow Warbler	-	1	0	2	0	1	1	3	7	**11**	0.030

Species Name	Percent Indicator Value										P-value
	Year 1	Year 2	Year 3	Year 4	Year 5	Year 6	Year 7	Year 8	Year 9	Year 10	
Tree Swallow	-	0	2	1	-	0	0	2	6	**11**	0.031
Orange-crowned Warbler	-	0	0	1	6	0	0	2	2	**11**	0.034
Nashville Warbler	0	2	6	4	5	0	4	4	3	11	0.141
California Towhee	-	-	-	-	-	-	2	-	-	5	0.204
Blue-gray Gnatcatcher	1	-	-	-	2	1	1	0	0	4	0.391
MacGillivray's Warbler	1	3	1	7	4	7	5	9	7	10	0.433
Bullock's Oriole	-	0	0	2	-	-	1	0	-	4	0.444
Acorn Woodpecker	1	1	0	0	0	-	2	4	1	5	0.492
Wrentit	1	0	0	0	1	0	2	0	0	4	0.61
Costa's Hummingbird	-	2	-	-	-	-	-	-	-	2	0.655
California Quail	1	0	-	1	2	-	2	0	-	3	0.802
Western Scrub-Jay	2	0	1	1	2	1	1	0	0	3	0.876
Spotted Towhee	4	5	5	8	8	5	5	4	3	8	0.915

Discussion

Black-backed Woodpecker Annual Occupancy

Our fourth year of surveys indicates that Black-backed Woodpeckers continue to be widely distributed across recent fire areas on the ten national forests in our study area, with the proportion of occupied fires and points higher in 2012 then in previous years. Point estimates of the percentage of occupied survey points within each year's sampling frame have varied across years: 25% in 2009, 19% in 2010, 21% in 2011, and 24% in 2012. An even greater increase this year was seen in the estimated percentage of occupied fires within the sampling frame: 60% in 2009, 65% in 2010, 48% in 2011, and 78% in 2012. Applied to the total amount of burned forest within each year's sampling frame, this results in 58,443 occupied hectares in 2009, 41,024 occupied hectares in 2010, 37,183 occupied hectares in 2011, and 67,208 occupied hectares in 2012. These quantities are only estimates, but will provide useful benchmarks for assessing future changes in Black-backed Woodpecker habitat and occupied areas in the Sierra Nevada.

Of particular interest is whether Black-backed Woodpecker occupancy within sampled fires in our study region is significantly changing from year to year. Based on the results of annual occupancy models, the total proportion of occupied points in 2010 was significantly lower than in 2009, indicating a drop in occupancy. In 2011, the proportion of occupied sites was not statistically different from that in 2010, and 95% confidence intervals overlap with estimates from 2009. In 2012, occupancy was significantly higher than 2010 and 2011, and on par with levels in 2009. Consequently, while total occupancy appears to have dropped from 2009 to 2010, it appears to have increased back to 2009-levels in 2012.

It is important, yet challenging, to disentangle changes in both the proportion of occupied fires and the proportion of occupied points. The sampling frame changes from year-to-year, so the proportion of occupied fires will likely be sensitive to this, and may partially or wholly account for the apparent significant drop in occupied fires in 2011 and rise in 2012. Across all four years of sampling, by comparison, the estimated proportion of occupied survey points has stayed within 19-25% (based on yearly means), showing greater stability as a metric. Because the proportion of occupied points is less sensitive to annual changes in the sampling frame and/or the randomly selected subset of the sampling frame that is actually sampled, it may be a superior index of long-term population size.

Black-backed Woodpecker Dynamic Occupancy

Point-level results. Our results from 4 years of data indicate strong differences between colonization and extinction dynamics of Black-backed Woodpeckers in burned forests. Average colonization probability (defined here as the probability of a single survey point becoming occupied by woodpeckers given that it was previously unoccupied subsequent to the fire) was quite low (8%), while average extinction probability was much higher (67%). The probability of a site being colonized was strongly positively associated with snag density and strongly negatively associated with fire age. By comparison, no single factor was as strongly associated with extinction, with a negative association with pre-fire canopy coverage and burn severity (i.e., greater pre-fire canopy cover and more severe fire made extinction less likely) garnering the strongest support.

*Fire-level results.*Given the large number of fires (87) sampled over at least one of the 4 survey years, it was possible in the present analysis to also examine which covariates correlated with the probability of colonization and extinction at fires (or at least the portion of each fire that we surveyed). Our results showed strong support for fire age as the main driver behind colonization – similar to the point-level results – and extinction as having a year-specific effect. Year-level extinction was only tested in the fire-level analysis, and its importance demonstrates that there is unexplored heterogeneity in extinction probabilities, perhaps due to weather or climate, that are driving year-to-year differences in extinction probability.

Combining both analyses of dynamic occupancy. The differences between the relative frequency of colonization versus extinction as well as the strength of covariate relationships of colonization versus extinction lead to novel insight on the drivers behind changes in Black-backed Woodpecker occurrence. Based on previous work (e.g., Siegel et al. 2011, Saracco et al. 2011), we tend to think of occurrence as being limited by fire age and snag density. This leads to the assumption that an occupied site may go extinct because the site has aged to a certain point, and that the critical age at which a site goes extinct depends on habitat quality characteristics, such as snag density.

Our results, however, strongly question this general framework. Since extinction probability was only moderately supported by any of the hypothesized factors (specifically burn severity and pre-fire canopy cover), extinction may best be considered a relatively likely event, but essentially a random one. That does not mean that other factors that were not investigated (e.g., post-fire management actions that change habitat) do not have an effect on extinction, but that extinction appears to occur with no strong relationship to the investigated covariates. By contrast, colonization (after fires are greater than 1 year old) is a relatively unlikely event, but one which is strongly associated with both fire age and snag density. Despite being unlikely, since overall point-level occupancy is only around 20 to 25% (see previous section), colonization is a relatively common occurrence. For example, given an overall occupancy of 20% and modeled average probabilities of colonization and extinction, assuming all sites have average covariate values, we would expect 11.5% of all sites (regardless of occupancy status) to go extinct in a given year and 5.8% of all sites to become colonized. Colonization after one year post-fire, consequently, is an important dynamic strongly influencing overall occupancy. If management actions were to be taken aimed at increasing overall occupancy, these results suggest that colonization should be targeted rather than extinction, presumably through the retention of early post-fire stands with high snag densities.

The importance of colonization as a driver of occurrence dynamics for Black-backed Woodpeckers in burned forests suggests a sort-of “grass is always greener” scenario, or more accurately, a “trees are always blacker” one. Black-backed Woodpeckers within our greater Sierra Nevada study area will may always have the potential to colonize younger post-fire forests, as adequately large fires burn in the region during most years. So, for a woodpecker inhabiting a 6-year old fire area, whether or not it moves to a newer fire area may not be determined by the characteristics of the site it currently occupies, but rather by whether there is a better, more recently burned site nearby to colonize. Thus extinction may not be a function of the patch itself, but a consequence of the proximity to desirable colonization options and the capacity to find them.

Multi-species Occupancy within Post-fire Forests

Our analyses strongly support the notion that bird communities change in a complex manner in the decade immediately post-fire. The results highlight that no single set of post-fire conditions will be beneficial to all members of post-fire bird communities. Rather, post-fire communities will be determined by fine-scale habitat and structural features defined by the intersection of fire age, burn severity, pre-fire vegetation, and presumably other topographical and environmental features.

Of particular focus in this analysis is the effect of fire age in structuring post-fire bird communities. While we found significant effects of burn severity, heterogeneity in burn severity, snag density, life tree density, and pre-fire canopy cover, the yearly effects of fires again seem to have a clear signal that can be interpreted at the level of the individual species. Specifically, ordination illustrated that bird communities change the most in the first 5 years post-fire, and then between years 5 and 10, the community stops changing in a linear fashion, with individual fires showing heterogeneity depending on their specific environmental features.

This finding was supported by indicator species analysis, which did not find strong year-specific associations for most species. When year-specific associations were found, they were found in years 2, 4, 5, and 10, again supporting the concept of rapid change in years 1-5, followed by slow change and turnover. As any one year is not altogether different from any other year, the finding of few year-specific indicator species is not particularly surprising. A stronger result would likely be found if years were grouped together (e.g., 1-2, 3-5, and 5-10 years post-fire) and/or were separated by environmental characteristics (e.g., burn severity).

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Appendix I.

List of all bird species identified during Black-backed Woodpecker passive surveys.

Common Name	Scientific Name	Family	4-Letter Code
Mountain Quail	*Oreortyx pictus*	Odontophoridae	MOUQ
California Quail	*Callipepla californica*	Odontophoridae	CAQU
Sooty Grouse	*Dendragapus fuliginosus*	Phasianidae	BGRO
Turkey Vulture	*Cathartes aura*	Cathartidae	TUVU
Osprey	*Pandion haliaetus*	Pandionidae	OSPR
Bald Eagle	*Haliaeetus leucocephalus*	Accipitridae	BAEA
Sharp-shinned Hawk	*Accipiter striatus*	Accipitridae	SSHA
Northern Goshawk	*Accipiter gentilis*	Accipitridae	NOGO
Red-tailed Hawk	*Buteo jamaicensis*	Accipitridae	RTHA
American Kestrel	*Falco sparverius*	Falconidae	AKES
Peregrine Falcon	*Falco peregrinus*	Falconidae	PEFA
Killdeer	*Charadrius vociferus*	Charadriidae	KILL
Band-tailed Pigeon	*Patagioenas fasciata*	Columbidae	BTPI
Mourning Dove	*Zenaida macroura*	Columbidae	MODO
Western Screech-Owl	*Megascops kennicottii*	Strigidae	WESO
Great Horned Owl	*Bubo virginianus*	Strigidae	GHOW
Northern Pygmy-Owl	*Glaucidium gnoma*	Strigidae	NOPO
Common Nighthawk	*Chordeiles minor*	Caprimulgidae	CONI
Common Poorwill	*Phalaenoptilus nuttallii*	Caprimulgidae	COPO
White-throated Swift	*Aeronautes saxatalis*	Apodidae	WTSW
Anna's Hummingbird	*Calypte anna*	Trochilidae	ANHU
Costa's Hummingbird	*Calypte costae*	Trochilidae	COHU
Calliope Hummingbird	*Stellula calliope*	Trochilidae	CAHU
Rufous Hummingbird	*Selasphorus rufus*	Trochilidae	RUHU
Lewis's Woodpecker	*Melanerpes lewis*	Picidae	LEWO
Acorn Woodpecker	*Melanerpes formicivorus*	Picidae	ACWO
Williamson's Sapsucker	*Sphyrapicus thyroideus*	Picidae	WISA
Red-breasted Sapsucker	*Sphyrapicus ruber*	Picidae	RBSA
Nuttall's Woodpecker	*Picoides nuttallii*	Picidae	NUWO
Downy Woodpecker	*Picoides pubescens*	Picidae	DOWO
Hairy Woodpecker	*Picoides villosus*	Picidae	HAWO
White-headed Woodpecker	*Picoides albolarvatus*	Picidae	WHWO
Black-backed Woodpecker	*Picoides arcticus*	Picidae	BBWO
Northern Flicker	*Colaptes auratus*	Picidae	NOFL
Pileated Woodpecker	*Dryocopus pileatus*	Picidae	PIWO
Olive-sided Flycatcher	*Contopus cooperi*	Tyrannidae	OSFL
Western Wood-Pewee	*Contopus sordidulus*	Tyrannidae	WEWP
Hammond's Flycatcher	*Empidonax hammondii*	Tyrannidae	HAFL
Gray Flycatcher	*Empidonax wrightii*	Tyrannidae	GRFL

Common Name	Scientific Name	Family	4-Letter Code
Dusky Flycatcher	*Empidonax oberholseri*	Tyrannidae	DUFL
Pacific-slope Flycatcher	*Empidonax difficilis*	Tyrannidae	PSFL
Black Phoebe	*Sayornis nigricans*	Tyrannidae	BLPH
Ash-throated Flycatcher	*Myiarchus cinerascens*	Tyrannidae	ATFL
Western Kingbird	*Tyrannus verticalis*	Tyrannidae	WEKI
Cassin's Vireo	*Vireo cassinii*	Vireonidae	CAVI
Hutton's Vireo	*Vireo huttoni*	Vireonidae	HUVI
Warbling Vireo	*Vireo gilvus*	Vireonidae	WAVI
Gray Jay	*Perisoreus canadensis*	Corvidae	GRAJ
Steller's Jay	*Cyanocitta stelleri*	Corvidae	STJA
Western Scrub-Jay	*Aphelocoma californica*	Corvidae	WESJ
Pinyon Jay	*Gymnorhinus cyanocephalus*	Corvidae	PIJA
Black-billed Magpie	*Pica hudsonia*	Corvidae	BBMA
Clark's Nutcracker	*Nucifraga columbiana*	Corvidae	CLNU
American Crow	*Corvus brachyrhynchos*	Corvidae	AMCR
Common Raven	*Corvus corax*	Corvidae	CORA
Purple Martin	*Progne subis*	Hirundinidae	PUMA
Tree Swallow	*Tachycineta bicolor*	Hirundinidae	TRES
Violet-green Swallow	*Tachycineta thalassina*	Hirundinidae	VGSW
Cliff Swallow	*Petrochelidon pyrrhonota*	Hirundinidae	CLSW
Mountain Chickadee	*Poecile gambeli*	Paridae	MOCH
Chestnut-backed Chickadee	*Poecile rufescens*	Paridae	CBCH
Oak Titmouse	*Baeolophus inornatus*	Paridae	OATI
Juniper Titmouse	*Baeolophus ridgwayi*	Paridae	JUTI
Bushtit	*Psaltriparus minimus*	Aegithalidae	BUSH
Red-breasted Nuthatch	*Sitta canadensis*	Sittidae	RBNU
White-breasted Nuthatch	*Sitta carolinensis*	Sittidae	WBNU
Pygmy Nuthatch	*Sitta pygmaea*	Sittidae	PYNU
Brown Creeper	*Certhia americana*	Certhiidae	BRCR
Rock Wren	*Salpinctes obsoletus*	Troglodytidae	ROWR
Canyon Wren	*Catherpes mexicanus*	Troglodytidae	CANW
Bewick's Wren	*Thryomanes bewickii*	Troglodytidae	BEWR
House Wren	*Troglodytes aedon*	Troglodytidae	HOWR
Pacific Wren	*Troglodytes pacificus*	Troglodytidae	PAWR
Blue-gray Gnatcatcher	*Polioptila caerulea*	Polioptilidae	BGGN
American Dipper	*Cinclus mexicanus*	Cinclidae	AMDI
Golden-crowned Kinglet	*Regulus satrapa*	Regulidae	GCKI
Ruby-crowned Kinglet	*Regulus calendula*	Regulidae	RCKI
Western Bluebird	*Sialia mexicana*	Turdidae	WEBL
Mountain Bluebird	*Sialia currucoides*	Turdidae	MOBL
Townsend's Solitaire	*Myadestes townsendi*	Turdidae	TOSO
Hermit Thrush	*Catharus guttatus*	Turdidae	HETH

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American Robin	*Turdus migratorius*	Turdidae	AMRO
Wrentit	*Chamaea fasciata*	Timaliidae	WREN
European Starling	*Sturnus vulgaris*	Sturnidae	EUST
Orange-crowned Warbler	*Oreothlypis celata*	Parulidae	OCWA
Nashville Warbler	*Oreothlypis ruficapilla*	Parulidae	NAWA
Yellow Warbler	*Setophaga petechia*	Parulidae	YWAR
Yellow-rumped Warbler	*Setophaga coronata*	Parulidae	AUWA
Black-throated Gray Warbler	*Setophaga nigrescens*	Parulidae	BTYW
Townsend's Warbler	*Setophaga townsendi*	Parulidae	TOWA
Hermit Warbler	*Setophaga occidentalis*	Parulidae	HEWA
MacGillivray's Warbler	*Geothlypis tolmiei*	Parulidae	MGWA
Common Yellowthroat	*Geothlypis trichas*	Parulidae	COYE
Wilson's Warbler	*Cardellina pusilla*	Parulidae	WIWA
Green-tailed Towhee	*Pipilo chlorurus*	Emberizidae	GTTO
Spotted Towhee	*Pipilo maculatus*	Emberizidae	SPTO
California Towhee	*Melozone crissalis*	Emberizidae	CALT
Chipping Sparrow	*Spizella passerina*	Emberizidae	CHSP
Brewer's Sparrow	*Spizella breweri*	Emberizidae	BRSP
Black-chinned Sparrow	*Spizella atrogularis*	Emberizidae	BCSP
Vesper Sparrow	*Pooecetes gramineus*	Emberizidae	VESP
Lark Sparrow	*Chondestes grammacus*	Emberizidae	LASP
Black-throated Sparrow	*Amphispiza bilineata*	Emberizidae	BTSP
Sage Sparrow	*Amphispiza belli*	Emberizidae	SAGS
Fox Sparrow	*Passerella iliaca*	Emberizidae	FOSP
Song Sparrow	*Melospiza melodia*	Emberizidae	SOSP
Lincoln's Sparrow	*Melospiza lincolnii*	Emberizidae	LISP
White-crowned Sparrow	*Zonotrichia leucophrys*	Emberizidae	WCSP
Dark-Eyed Junco	*Junco hyemalis*	Emberizidae	DEJU
Western Tanager	*Piranga ludoviciana*	Cardinalidae	WETA
Black-headed Grosbeak	*Pheucticus melanocephalus*	Cardinalidae	BHGR
Lazuli Bunting	*Passerina amoena*	Cardinalidae	LAZB
Red-winged Blackbird	*Agelaius phoeniceus*	Icteridae	RWBL
Western Meadowlark	*Sturnella neglecta*	Icteridae	WEME
Brewer's Blackbird	*Euphagus cyanocephalus*	Icteridae	BRBL
Brown-headed Cowbird	*Molothrus ater*	Icteridae	BHCO
Bullock's Oriole	*Icterus bullockii*	Icteridae	BUOR
Purple Finch	*Carpodacus purpureus*	Fringillidae	PUFI
Cassin's Finch	*Carpodacus cassinii*	Fringillidae	CAFI
House Finch	*Carpodacus mexicanus*	Fringillidae	HOFI
Red Crossbill	*Loxia curvirostra*	Fringillidae	RECR
Pine Siskin	*Spinus pinus*	Fringillidae	PISI
Lesser Goldfinch	*Spinus psaltria*	Fringillidae	LEGO

Common Name	Scientific Name	Family	4-Letter Code
Lawrence's Goldfinch	*Spinus lawrencei*	Fringillidae	LAGO
American Goldfinch	*Spinus tristis*	Fringillidae	AMGO
Evening Grosbeak	*Coccothraustes vespertinus*	Fringillidae	EVGR