



Chaparral bird community responses to prescribed fire and shrub removal in three management seasons

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Abstract

1. Chaparral, a type of shrubland common throughout the California Floristic Province, is subject to management and removal in regions where wildfire threatens human lives and property. Management practices include conducting prescribed burns outside of the historical fire season and employing mechanical fuel reduction (mastication). As the wildland–urban interface grows, particularly in coastal California, more of this ecosystem is subject to active management.
2. To understand the ecological implications of current California chaparral fire management practices, we studied bird species composition, abundance and foraging guilds in managed and unmanaged chaparral over 5 years. Study areas were located in Mendocino County in the coast ranges of northern California. We contrast six chaparral removal or “fuels manipulation” treatments: (1) fall fire, (2) winter fire, (3) spring fire, (4) fall mastication, (5) spring mastication and (6) untreated control. Treatments and controls were implemented in plots 2 ha or larger, and replicated four times each.
3. We find that species richness in prescribed fire treatments reaches comparable levels to controls in the first 3 years following treatment, whereas masticated units always have lower species richness. Generalized linear mixed models additionally confirm that mastication has highly negative effects on observed abundances of birds compared to controls and to prescribed fire.
4. The season in which fuels reduction occurred was less important to species richness, although fall fire was more beneficial to bird abundance than spring or winter fire. Fire treatments in all seasons maintain the same general bird community structure as controls, while mastication results in strongly differentiated assemblages, increasing granivores while nearly excluding foliage gleaners.
5. *Synthesis and applications.* We compare two California chaparral management techniques, prescribed fire and mastication, in three seasons (fall, winter and spring) in northern California, USA. We tracked chaparral bird community response in 23 experimental units for 2–5 years. We conclude that prescribed fire and mastication are not interchangeable management techniques, and that mastication negatively

impacts bird communities, altering guild structure and reducing both diversity and abundance.

KEYWORDS

bird communities, California chaparral, California Floristic Province, Fire and Fire Surrogates, mastication, prescribed fire, shrublands, wildfire management

1 | INTRODUCTION

California chaparral, a unique and diverse set of Mediterranean-climate shrub communities restricted to the California Floristic Province (CFP), is one of the most fire-prone ecosystems in North America. California chaparral extends over much of California, extreme southwestern Oregon and northwestern Baja California and is characterized by sclerophyllous vegetation, high local and regional species diversity and high levels of endemism among both plants and animals (Keeley & Davis, 2007). Chaparral harbours a major fraction of the biodiversity of the CFP (identified as a biodiversity hotspot; Conservation International, 2011, Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000). Of the 4,846 native species of vascular plants in the CFP, 24% (or 1,177) are present in chaparral (Halsey & Keeley, 2016), and of these, 44% are considered rare (Keeley, 2005).

Chaparral is also the most suburbanized habitat in California (with the possible exception of coastal scrub); the wildland–urban interface in California currently contains over 5 million housing units (Radeloff et al., 2005), with the development pressures in chaparral and areas of very high fire risk predicted to only increase (Hammer, Stewart, & Radeloff, 2009; Mann et al., 2014). While fire poses a threat to human lives and property, too-frequent fire and degradation of chaparral ecosystems for agriculture and fire management are causing extreme losses of biodiversity in this ecosystem (Keeley, 2002, 2006; Stylinski & Allen, 1999). These factors combined pose major challenges for fire managers. Balancing conservation priorities with human health and safety require targeted studies evaluating both the efficacy of vegetation management techniques in reducing fire risk and their effects on biodiversity. These challenges are not unique to California; similar issues exist for ecological consequences of fuel management in other xeric or Mediterranean sclerophyll scrublands elsewhere in the world, such as in Europe and Australia (Brotos, Pons, & Herrando, 2005; Herrando, Brotos, & Llacuna, 2002; Woinarski, 1999).

In California today, chaparral fire management practices do not reproduce historical fire regime norms. Wildfire risk, concerns about smoke and public health, political and economic pressures and regulations at many levels often force land managers who use prescribed burns to conduct them outside of the historical fire season (Knapp, Estes, & Skinner, 2009). In California and elsewhere, managers increasingly replace prescribed fire with mechanical crushing of vegetation known as “mastication.” Although both prescribed fire and mastication are used widely throughout the range of California chaparral, there are few studies focusing on prescribed fire effects in this habitat (Beyers & Wakeman, 2000; Lawrence, 1966; Potts, Marino, & Stephens, 2010; Potts & Stephens, 2009). Targeted studies on the effects of mastication on chaparral communities indicate that exotic invasives

and annual grasses are more prevalent after the treatment (Bradley, Gibson, & Bunn, 2006; Potts & Stephens, 2009; and see Coulter, Southworth, & Hosten, 2010 for work outside California in the CFP), reducing native diversity (Stylinski & Allen, 1999) and, counter to the intention, increasing fire frequency (D'Antonio, 2000).

Of the fire characteristics that have been evaluated, prescribed fire (Beyers & Wakeman, 2000) and season of burn (Coulter et al., 2010; Knapp et al., 2009; Potts & Stephens, 2009) are known to produce significant changes to the vegetation community, but there is a complete absence of comparative effects of season of prescribed fires on chaparral birds (Knapp et al., 2009). Research from southern California shows that wildfire in chaparral can alter bird community composition by changing habitat structure, food availability and predator movement (Lawrence, 1966; Mendelsohn et al., 2008; Wirtz, 1979, 1982), but such studies are limited. Studies of vertebrates in post-conversion chaparral (as by mastication) are similarly limited (Lillywhite, 1977), although recent work has shown strong negative effects of medium- to large-scale mastication projects on shrub-associated bird diversity (Seavy, Alexander, & Hosten, 2008).

This study was conducted part of a unique, controlled and replicated experiment conducted in 2001–2005 in northern California. Our project represents the first controlled experiment with replication comparing the effects of prescribed fire and mastication treatments in multiple seasons on the chaparral bird community. We contrast the effects on bird diversity and abundance of two chaparral fuels reduction treatments (prescribed fire and mastication) in three seasons (fall, winter and spring) and a comparison control. We expected bird diversity to recover to control-like assemblages in prescribed fire units, with fall fire (occurring in the historic wildfire season) recovering with the highest degree of similarity within the first few years post-treatment compared to other treatment seasons. Although the two chaparral treatments have not been directly compared previously, we expected differences in vegetation species composition and structure between treatment types, affecting what bird species use them (Appendix S1). We therefore expected masticated plots to have lower bird abundance and species richness compared to prescribed fire plots, and that treatment type would have larger effects than seasonality on bird biodiversity metrics and guild structure.

2 | MATERIALS AND METHODS

2.1 | The Fire and Fire Surrogates model

The Fire and Fire Surrogates Network is a group of large-scale studies across the United States in seasonally dry ecosystems, implemented

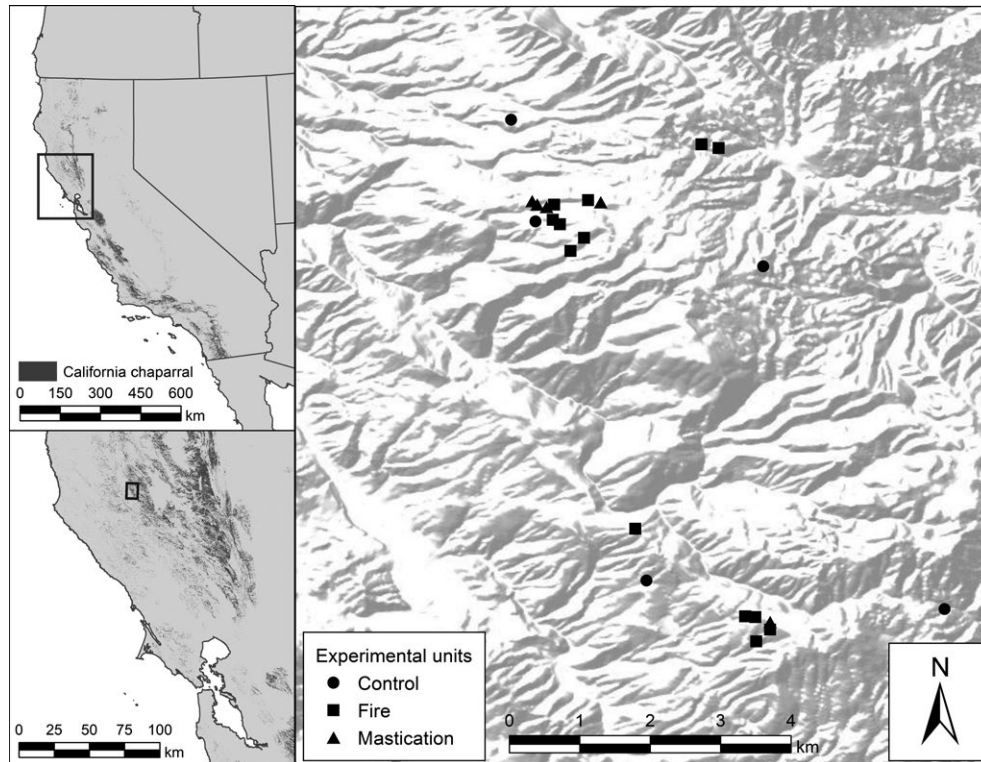


FIGURE 1 Locations of experimental units and coverage of California chaparral shrublands. Shrublands are represented in inset maps with wildlife habitat relationship data from the California GAP analysis project (US Geological Survey, 2011) and include all GAP California chaparral classes. Shading in right panel represents north (light)/south (dark) aspect of topography

to create a scientific basis for evaluating trade-offs between fuels management by prescribed fire and mechanical thinning, measuring fire behaviour during treatment and assessing effects on native and non-native biodiversity (McIver, Youngblood, & Stephens, 2009; Schwilk et al., 2009; Youngblood et al., 2005). Following this model, this California chaparral fuels manipulation experiment took place over 2001–2005 at the Hopland Research and Extension Center (HREC, managed by the University of California, Berkeley) and the nearby Red Mountain and Cow Mountain Recreation Area (both managed by the Bureau of Land Management) in the North Coast ranges of Mendocino County, California. All study plots are located within the northern California chaparral vegetation community, situated c. 50 km from the Pacific coast and 180 km north of San Francisco (Figure 1).

This experiment began in 2001 with pretreatment monitoring. Fire and mechanical treatments were conducted in 2002 and 2003. Post-treatment monitoring was conducted from 2002 to 2005. Project findings synthesize 5 years of replicated data on fuel recovery (Potts et al., 2010), non-native plant invasion and plant diversity (Potts & Stephens, 2009; Wilkin et al., 2014) and bird community response (this study; Appendix S1). Implementation of this project, including provision of research sites, permits and fire crews, was accomplished through collaboration between HREC, the Bureau of Land Management Ukiah Field Office (BLM) and the California Department of Forestry and Fire Protection (CAL FIRE) Mendocino and Lake County Units.

Mastication and prescribed fires created a homogeneous treatment, which removed or reduced 95%–100% of standing above-ground

biomass without damaging subsurface soil and root systems. Although the masticator-shredded vegetation into a <5 cm layer of small diameter (<2.5 cm) woody debris, prescribed fire treatments left some “skeletons” of surface-killed plants, maintaining some vertical structure (Figure 2). Treatments and controls were replicated four times for a total of 24 experimental units, each larger than 2 ha (details, dates of implementation and site descriptions are available in Appendix S2). Effects of management on bird communities may depend on the scale of treatment area, and we note that while 2 ha might be similar to area managed near houses, other management areas in California are much larger.

2.2 | Bird counts

Bird surveys were conducted in most of the vegetation management units and one additional control unit (five control, four spring fire, four winter fire, four fall fire, three spring mastication and three fall mastication units) for a total of 23 units. Two masticated units were not surveyed for birds due to accessibility issues. Bird community composition and abundance were estimated using a double-observer point count method (Nichols et al., 2000) with a detection cut-off of 50 m. This technique reduces observer bias: one observer stands at a fixed point for 10 min noting every bird detection (visual, call and song) as well as its distance from the observer, while the second observer records and adds the missed detections. Two point counts were conducted in each treatment unit, sequentially (for >46 points, due to opportunistic sampling in control areas), with

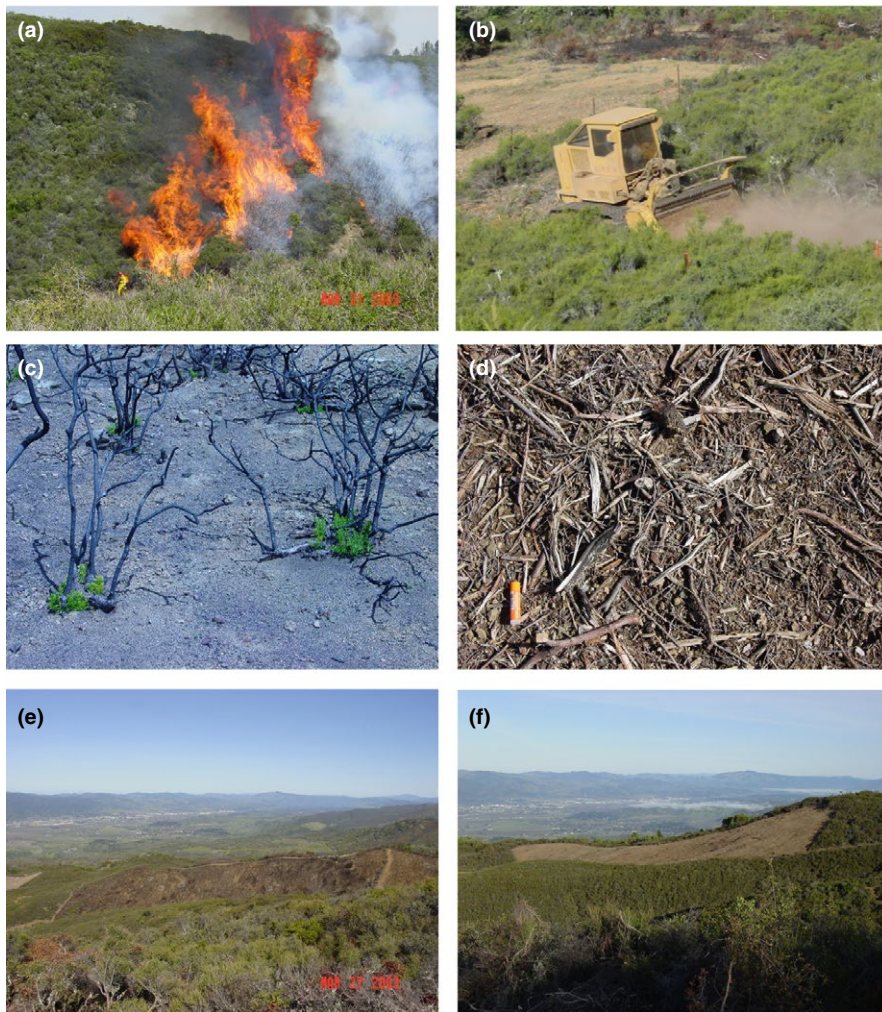


FIGURE 2 Prescribed fire (a) and mastication (b) treatments were carried out within 2 years. Above-ground vegetation biomass was reduced by 95% in both types of treatments. Remaining fuel beds were characterized by dead plant “skeletons” for prescribed fire (c) and ≤ 5 cm length shredded, woody debris for mastication treatments (d). A representative post-management experimental unit for prescribed fire (e) and mastication (f) are shown

a distance of at least 100 m separating the points. Points placed at this distance within chaparral stands can be considered independent due to the extreme density of vegetation leading to low detection radii. For consistency, only two observers (Vaughn and Potts) performed the point counts over the entire study period.

Point counts were conducted 4–7 times per year in each experimental unit, with scheduled visits distributed throughout the year: once in winter, each month in spring/early summer and once in fall (Appendix S3). All counts were conducted within the first 4 hr of daylight, with all sites visited over a several day period within each seasonal sampling window. Experimental units were visited in a random order to reduce time-of-day bias. No counts were performed in heavy rain, fog or windy conditions. As fuel reduction treatments were implemented over 2 years, we collected bird point count data in each experimental unit for between 1.5 and 4.5 years.

2.3 | Data analysis

2.3.1 | Species richness and similarity comparisons

Species richness is the count of all species present within an experimental unit and is a reliable metric for comparing biodiversity between

the treatment types and seasons. We employed rarefaction methods to correct for sampling bias introduced by uneven sampling effort. Rarefaction and species richness estimations were performed 200 replicates and without replacement to create meaningful variance estimates. Each point count was considered one data point. Time since treatment was not considered. Sample-based rarefaction and estimation of variance were performed first, followed by replotting on an x-axis of individual abundances instead of number of samples (Gotelli & Colwell, 2001, 2011). This method allows direct comparison of species richness between sample sets with very different abundances (Gotelli & Colwell, 2011).

Mean species richness resulting from rarefaction was then compared between treatment seasons with unpaired two-tailed Welch's *t* tests, with a null hypothesis that management does not change mean species richness compared to the control, and the alternative hypothesis that management changes the mean. Welch's *t* tests assess statistical significance when variances between samples are unequal. These tests were standardized by applying them at comparable numbers of individuals between control and treatment, at the number of individuals associated with extrapolated rarefaction estimates on twice the number of surveys performed (Hsieh, Ma, & Chao, 2016), and were then followed by Bonferroni corrections to conservatively

assess the true statistical significance levels of the multiple comparisons performed.

We calculated an abundance-based dissimilarity metric, the Morisita–Horn index (C_{mH}), for all pairwise comparisons of experimental units by treatment type and season. The C_{mH} ranges from 0 (no overlap in communities) to 1 (full overlap of communities) and is relatively unaffected by sample size and diversity (Wolda, 1981).

2.3.2 | Guild analyses

We classified bird species into five functional guilds (De Graaf, Tilgman, & Anderson, 1985): feeding guilds by main source of calories (nectarivores, insectivores, granivores, bird predators and “multiple,” comprising omnivores and birds that switch dietary preferences seasonally); preferred feeding substrate (ground, foliage gleaning, aerial, bark and “aerial,” comprising hovering, true aerial and flycatching); resident status (summer breeding, year-round, migration and winter non-breeding); breeding status (breeding and non-breeding); and nesting guilds among birds that breed in this area (tree, shrub, ground and cavity) for analysis (guild designations from Birds of North America Online, <http://bna.birds.cornell.edu/bna/>; the Cornell Lab of Ornithology, 2015 online bird guide, <http://www.allaboutbirds.org/guide>) and breeding observations recorded at HREC (Vaughn & Keiffer, 2007, Appendix S4).

Count data for bird individuals were aggregated across years and analysed by guild response in the immediate post-treatment time-frame. For each of the five categories, the proportions of bird individuals in each guild were compared between treatment–season experimental units using Pearson’s chi-squared test for count data with Yeats’ continuity correction or Fisher’s exact test for small sample sizes, with the hypothesis that proportions of individuals in each guild do not differ between control and treated units.

2.3.3 | Modelling observed bird abundances

We constructed a Poisson-distributed generalized linear mixed model (GLMM; Bolker et al., 2009) to analyse total bird detections per survey within our experimental design. We tested three fixed effects central to our hypotheses: (1) treatment type (prescribed fire, mastication, control), (2) treatment season (fall, winter, spring or “none” corresponding to the control) and (3) growth period, that is, an index of the number of years (turning over in January) since treatment or first surveys in the case of controls. For example, a plot that was treated in September

would be surveyed in growth period 0 until January of the following year (4 months total), at which point surveys are considered to be in growth period 1.

Three interactions among fixed effects were also included: (1) fire*fall, an interaction to test whether or not fall surveys were different between fire and mastication treatments; (2) fire*grow, an interaction to see if the effects of growth season differed between fire and control and (3) mast*grow, an interaction to test if the effects of growth season differed between mastication and control. Non-nested random effects measured during the study were included: (1) location (Cow Mountain, Red Mountain or Hopland), (2) count season (“ctseason,” winter, spring, summer or fall) and (3) calendar year in which the survey occurred (as a proxy for interannual variation in climate conditions). Vegetation surveys occurred too infrequently to include variables related to shrub cover and height; however, an interaction between growth period and treatment type was included to serve as a proxy for vegetation regrowth (details in Appendix S5).

Data were analysed and manipulated in R (version 3.2.1) using the packages “stats” (R Core Team, 2015), “pscl” (Jackman, 2015; Zeileis, Kleiber, & Jackman, 2008) and “MASS” (Venables & Ripley, 2002). Rarefaction and Morisita–Horn analyses were then carried out in EstimateS version 9.0 (Colwell, 2013). GLMM analysis was conducted in R using the package “lme4” (Bates, Maechler, Bolker, & Walker, 2014).

3 | RESULTS

3.1 | Bird survey results

A total of 49 bird species and 2,529 total bird individual detections were made in 354 point-count surveys (Appendix S6, Table S1). Survey effort differed greatly between masticated plots and other types of plots. Fall mastication sites were visited far fewer times than prescribed fire and control units because of accessibility issues (Table 1). Control plots were surveyed for an additional year prior to vegetation management activity and visited 123 times in total. The vast majority (99%) of detections recorded during point counts were ≤ 10 m from observers, which supports the independence of point counts separated by 100 m in dense shrub (Appendix S7). Raw counts of abundances per survey show generally increasing numbers of birds detected in prescribed fire units in all seasons, while masticated units show relatively low-observed abundance in all post-treatment growth periods for both treatment seasons (Figure 3).

TABLE 1 Number of surveys conducted in each treatment type by season, followed by number of unique points surveyed in each combination [in brackets]. Exact coordinates of some control points were not recorded due to opportunistic sampling in these areas

Treatment season	Treatment type			Totals
	Control	Fire	Mastication	
None	123 [20]	–	–	123 [20]
Winter	–	69 [8]	–	69 [8]
Spring	–	57 [8]	23 [6]	80 [14]
Fall	–	66 [8]	16 [6]	82 [14]
Total	123 [20]	192 [24]	39 [12]	354 [56]

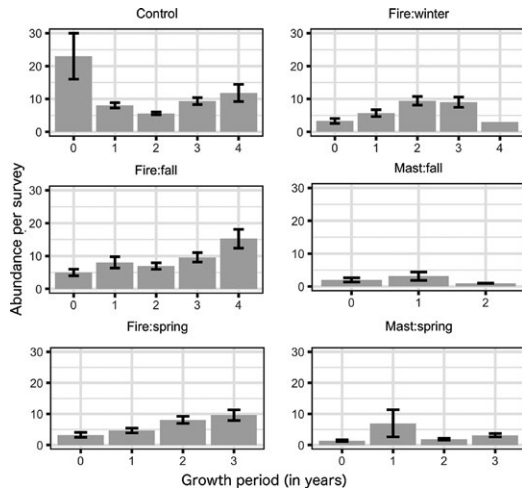


FIGURE 3 Observed bird abundances per point count in all experimental units by growth period. Error bars represent 1 SEM. No error bar could be calculated for winter fire treatments in growth period 5 due to low sample size

Treatments differed strongly by their most abundant species detected (Appendix S6, Table S1). In control units, the most detected birds were Wrentit (*Chamaea fasciata*), California Scrub Jay (*Aphelocoma californica*) and Lesser Goldfinch (*Spinus psaltria*), followed by Spotted Towhee (*Pipilo maculates*). Fire-treated plots show high similarity to controls in all seasons, with Wrentit, California Scrub Jay and Spotted Towhee also ranking among the most observed (Appendix S6, Table S2). Fall and spring fire also contained high numbers of Bewick’s Wrens (*Thryomanes bewickii*), while control and winter fire plots shared high numbers of Bell’s Sparrows (*Artemisiospiza belli*). In contrast, masticated plots had Bewick’s Wrens, Dark-eyed Juncos (*Junco hyemalis*) and Western Bluebird (*Sialia mexicana*) as the most commonly detected species, with fall mastication additionally having high numbers of California Quail (*Callipepla californica*). Ranked abundance comparisons (Appendix S6, Table S3) show that prescribed fire maintains the same dominant species as controls, and mastication does not. This conclusion is further supported by the calculations of the C_{mH} (Table 2), comparing similarity among bird communities in all experimental units.

3.2 | Species richness and similarity comparisons

Species richness varied greatly among treatment types, with prescribed fire units showing much higher richness than masticated units,

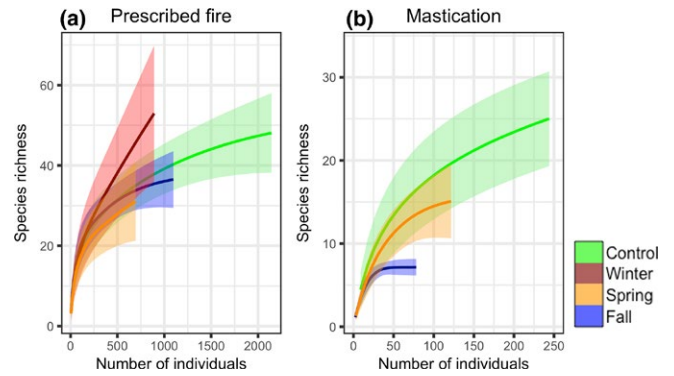


FIGURE 4 Species richness compared between controls and (a) prescribed fire and (b) mastication in all seasons. Prescribed fire treatments recovered to or exceeded control-like levels of species richness post-treatment, whereas masticated treatment areas always had lower species richness. Rarefaction was extrapolated to twice the number of surveys for all treatments and rescaled to number of individuals to account for sample density. Shaded areas represent 95% confidence intervals around estimated species richness (solid lines)

and masticated units falling well below the control levels of richness (Figure 4). Welch’s unpaired t tests were applied to estimates of species richness generated by rarefaction methods for each management scenario, while controlling for similar number of individuals (this is equivalent to assessing differences in species richness between controls and treatments at vertical lines drawn at maximum number of individuals plotted for each management case on Figure 4). Post hoc comparisons using Bonferroni corrections (with $p = .05$ significance level and $n = 5$ comparisons, $p_{corr} = .01$) indicated that the mean species richness for each treatment season was highly statistically different from the control in each case (Appendix S8). Prescribed fire units recovered richness comparable to control units within 3 years, with winter fire treatments having the highest diversity of birds in plots and exceeding species richness in controls. Fall fire had 91% of control-level species richness (Welch’s $t(2,174) = 25.75, p < .0001$), spring fire had 89% of the species richness of controls (Welch’s $t(1,133) = 17.95, p < .0001$) and winter fire had 140% (Welch’s $t(1,117) = 49.04, p < .0001$). In contrast, masticated units had much lower richness than controls, with fall mastication having much lower richness than spring mastication. Fall mastication produced 43% of control-level species richness (Welch’s $t(82) = 31.15, p < .0001$) and spring mastication resulted in 75% of species richness compared to controls (Welch’s $t(273) = 16.37, p < .0001$).

	Control	Fire: fall	Fire: winter	Fire: spring	Mastication: fall
Fire: fall	0.87	—	—	—	—
Fire: winter	0.923	0.864	—	—	—
Fire: spring	0.873	0.879	0.919	—	—
Mastication: fall	0.175	0.339	0.139	0.223	—
Mastication: spring	0.293	0.514	0.273	0.308	0.651

TABLE 2 Morisita–Horn indices of similarity of bird communities among experimental treatments. The Morisita–Horn index takes on values between 0 (no overlap) and 1 (full overlap of communities)

Comparisons of abundance structure of bird communities between experimental treatments and seasons with the C_{mH} show highest similarity between control and winter fire units ($C_{mH} = 0.923$), with control and spring fire then fall fire being next most similar ($C_{mH} = 0.873$ and $C_{mH} = 0.87$ respectively). Both spring and fall mastication showed very low similarity to controls ($C_{mH} = 0.293$ and $C_{mH} = 0.175$ respectively), with fall mastication and control representing the lowest similarity values across all treatment-season combinations (Table 2).

3.3 | Guild analyses

All five categories of bird guilds studied were found to be differentially impacted by treatment types and seasons (Figure 5). Compared to controls, masticated units attracted granivores over insectivores and reduced the proportions of omnivores and birds that utilize multiple food sources

(chi-squared test of proportions, $p < .0001$ for spring and fall). Spring masticated units attracted higher proportions of non-breeding birds than controls ($p < .0001$). Masticated units in both seasons were used by higher proportions of ground-nesting and ground-foraging birds and correspondingly lower proportions of tree-nesting and foliage-gleaning birds ($p < .0001$ spring, $p < .0001$ fall). In almost every test, masticated plots had statistically significantly different guild structure compared to control plots (Figure 5; Appendix S4, Table S2).

In contrast, prescribed fire treatments did not differ as sharply from controls in guild composition, and season was more important in structuring the guilds than was the case for masticated plots (Figure 5). Fall fire had more differences from controls, including feeding and foraging guild structure (compared to controls: more granivores, fewer insectivores; more ground feeders and fewer foliage gleaners, similar to mastication treatment plots; $p = .003$), and differences in nesting guilds,

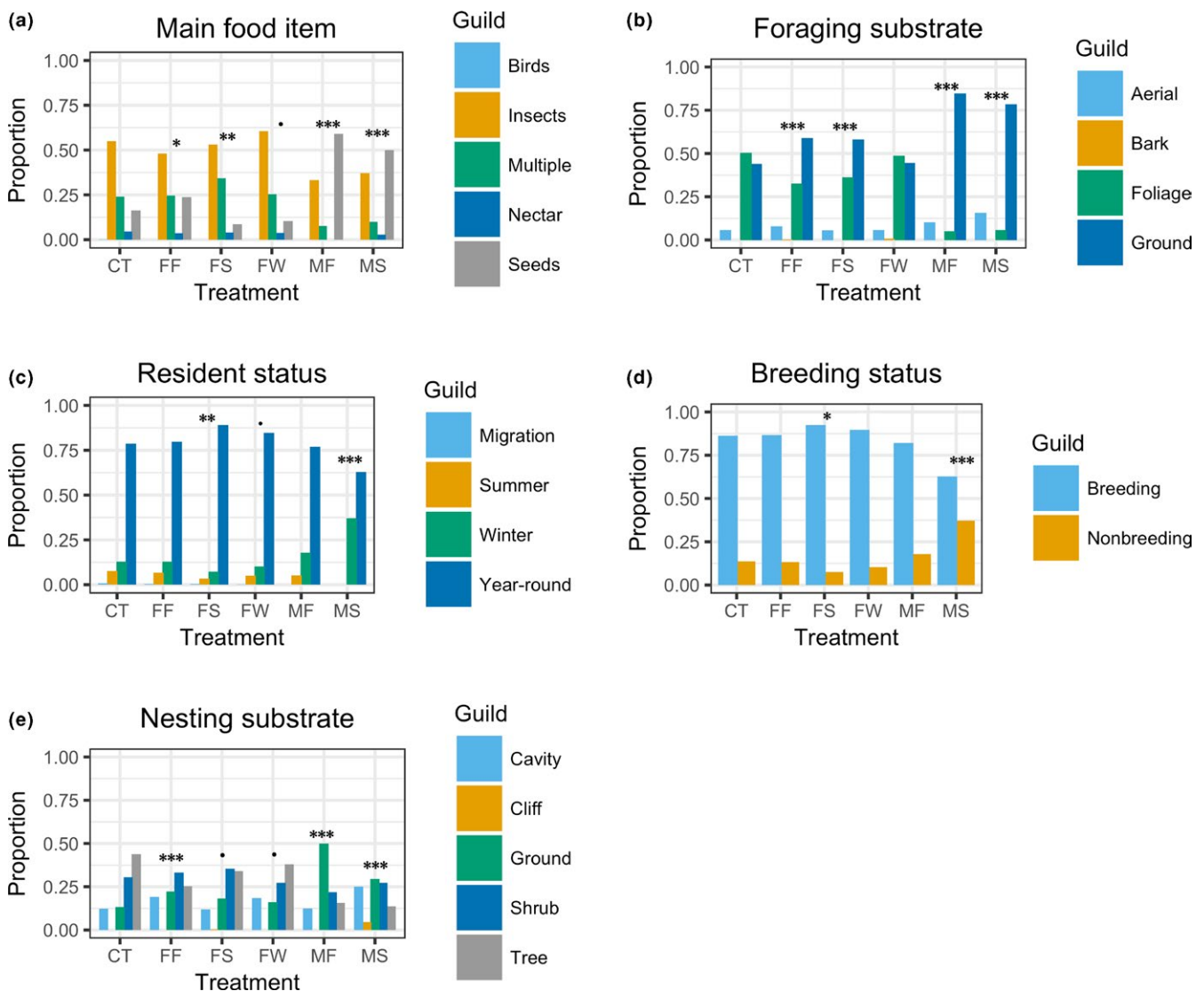


FIGURE 5 Proportions of birds in each guild by the following categories: (a) main food item, (b) foraging substrate, (c) resident status, (d) breeding status (whether or not a species breeds in the region) and (e) nesting substrate. Controls (CT) and treatments are prescribed fire in the fall, winter and spring (FF, FW and FS respectively) and mastication in the fall and spring (MF, MS). Chi-squared tests for significance (followed by Fisher’s exact test, where necessary) were performed on each group of proportions. Significance level codes are: $\leq .0001$ “***”; $\leq .001$ “**”; $\leq .01$ “*”; $\leq .05$ “.”

including fewer tree-nesters than controls ($p < .0001$). Winter fire treatments were the most similar to controls, while spring fire treatments resulted in differences in all categories examined. Compared to controls, spring fire had more birds that feed on multiple food sources, more ground feeders and fewer foliage gleaners ($p < .0001$), more visitations by year-round residents ($p = .0002$), more breeding birds ($p = .003$) and fewer tree-nesters ($p < .090$).

3.4 | Modelling observed bird abundances

Observed bird abundances per survey varied substantially between experimental unit types (Figure 3). GLMM analysis (Table 3) showed that (1) fire-treated units had fewer birds than controls ($p < .001$); (2) masticated units had fewer birds than either controls ($p < .001$) or fire-treated units ($p < .001$); (3) when fire was applied in the fall, it led to higher bird abundance ($p = .033$); (4) when fire was done in the winter, it may have led to higher bird abundance ($p = .057$); (5) bird abundance increased with the number of growth seasons for fire ($p < .001$), while the number of growth seasons had no effect on control ($p = .393$) or masticated ($p = .502$) plots and finally, (6) year-to-year variation was about twice as great as either site-to-site or season-to-season variation ($\sigma_{\text{year}}^2 = 0.076$, $\sigma_{\text{site}}^2 = 0.030$, $\sigma_{\text{season}}^2 = 0.026$).

4 | DISCUSSION

4.1 | Effects of management on chaparral bird communities

Our results provide the first direct comparison of the effects of two fuels manipulation treatments, prescribed fire and mastication, on California chaparral bird communities. Our primary finding is that mastication has very different effects on bird communities compared to prescribed fire and relative to controls. We found that prescribed fire treatments were more similar to controls in terms of species richness, abundance, community similarity and guild structure than masticated treatments. In contrast, mastication, compared to controls, lowers richness and overall abundances of bird species, changes the dominant

species of birds and alters guild structure by excluding insectivores, migratory and breeding birds. Although prescribed fire units had increasing bird abundances over successive seasons, masticated units did not show similar increases over time. Bird communities recover to control-like assemblages within 3–4 years after prescribed fire in any season but do not recover in masticated units. These effects on the bird community are likely mediated by the structure and species composition of the treated vegetation. Our results support our earlier hypothesis that the bird community is affected by the structure of vegetation resulting (and recovering) from treatment; however, further studies relating the bird and vegetation communities would be required to establish that this hypothesis is correct.

Secondarily (and consistent with plant community studies at these sites), we expected and found that treatment type would have a stronger effect on structuring the bird community than season of treatment. Season of treatment appears to have a limited affect, particularly for prescribed fire. In terms of total avian abundance, fall fire had the highest abundance compared to all other treatments, but winter fire had both the highest community similarity to controls and had greater estimated species richness.

For every metric evaluated, masticated units in both seasons were the most different from controls. Mastication affects bird communities in very different and generally negative ways compared to prescribed fire. Mastication is therefore not a substitute for prescribed fire as ecological management in chaparral. This finding differs from similar studies in other types of seasonally dry forests, where mastication may be a useful substitute for prescribed fire (with regards to bird communities) given management constraints (Fontaine & Kennedy, 2012). However, our results strongly support similar findings of negative impacts on shrubland-associated birds in chaparral by Seavy et al. (2008) and may be consistent with Alexander, Seavy, and Hosten (2007)'s finding that hand-pile and burn practices impact bird communities less than mastication. We also note that bird species' responses may differ on landscapes with larger treatment patches than we were capable of experimentally manipulating.

4.2 | Generalizability of the California chaparral fuels manipulation study

Previous work in California chaparral has been restricted to wildfire effects in southern California. Evidence suggests that wildfire and prescribed fire effects are not interchangeable (Alba, Skálová, McGregor, D'Antonio, & Pyšek, 2015), so the evaluation of prescribed fire as a management tool should not solely rely on studies following wildfire. Although the exact role of fire in chaparral likely varies across the region, it is clear that understanding its ecological effects throughout the entire range of chaparral and for taxa in addition to plants will be critically important to conservation efforts, as wildfire in California chaparral is predicted to increase with climate change (Batllori, Parisien, Krawchuk, & Moritz, 2013). An increase in fire sizes will likely affect the wildlife metacommunities, limiting refugia in wildfires (Mendelsohn et al., 2008) and affecting dispersal into and recolonization of burned areas (Brotons et al., 2005; van Mantgem, Keeley,

TABLE 3 Fixed effect parameter estimates from generalized linear mixed model (GLMM) analysis of observed bird abundances. Significant parameters are printed in bold

Parameter	Point estimate	SE	p-value
Intercept	2.357	0.221	<.001
Fire	-0.811	0.136	<.001
Mastication	-1.116	0.232	<.001
Fall	-0.340	0.228	.136
Winter	0.140	0.073	.057
Growth season	-0.051	0.060	.393
Fire × fall	0.537	0.252	.033
Fire × growth period	0.175	0.041	<.001
Mastication × growth period	-0.071	0.106	.502

& Witter, 2015). Management in California chaparral may also lead to the replacement of shrubland-associated birds with common suburban birds capable of transmitting Lyme disease bacteria, with consequences for disease ecology in California (Newman et al., 2015). More studies on chaparral wildlife and their interactions with a variety of fire characteristics and post-fire landscapes in California and elsewhere (Bolger, Scott & Rotenberry, 1997; Tingley, Ruiz-Gutiérrez, Wilkerson, Howell, & Siegel, 2016) are needed to assess consequences of the management for conservation and public health.

California chaparral has many similarities with Mediterranean scrublands elsewhere in the world and often shares their management challenges. The Fire and Fire Surrogates model employed here might productively be adapted to other systems where prescribed fire management and mechanical fuels treatments affect wildlife habitat, or where less is known about the interaction of the fire regime with wildlife (Woinarski, 1999). However, we caution against interpreting these results as directly applicable to such scrublands due to the many differences among them in human land-use history, fire ecology and avifaunas (e.g. Herrando et al., 2002). Although controlled ecological experiments are expensive and logistically challenging, the Fire and Fire Surrogates model is a strong inferential framework which would provide much knowledge if replicated in other shrubland ecosystems around the world.

5 | CONCLUSIONS

Comparative effects of fire management types and seasons on wildlife communities are essential to understanding the management trade-offs. The information provided in this study is important for chaparral managers who rarely have information about relative impacts of fuels treatments on wildlife, but must consider the persistence of wildlife species to make science-based management choices (Christensen et al., 1996).

Due to a lack of formal legal protections for chaparral in California, management activities are often implemented without adequate knowledge of direct and indirect ecological impacts to wildlife, and assessing the health of wildlife populations is in turn impeded by a lack of management data. Our results indicate that where fuels treatment management in chaparral is deemed necessary, prescribed fire will minimize diversity loss for bird communities compared to mastication, with fall or winter fire likely having the lowest impacts. However, prescribed fire is not necessary for the maintenance of chaparral biodiversity, and mastication may be more effective for fuels reduction (Appendix S1). All fuels management in chaparral has the potential to severely degrade habitat with repeated use. An ecologically conservative approach to lowering fire management impacts on wildlife communities would therefore be to (1) limit fire management to where there is a clear and demonstrated conflict with human habitation (this will likely take the form of mastication for safety reasons), (2) plan development and manage risk to human habitation rather than managing natural areas (Syphard et al., 2016) and (3) create a chaparral management inventory system to allow

scientists and managers to assess changes to the vegetation community due to management.

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AUTHORS' CONTRIBUTIONS

S.L.S. and J.B.P. designed and implemented the original experiment; J.B.P. and C.V. conducted all field surveys; E.A.N. and M.W.T. carried out all statistical analyses; E.A.N. wrote the manuscript and supporting information. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.mt3tr> (Newman, Potts, Tingley, Vaughn, & Stephens, 2017).

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